Linking individual variation in foraging behaviour and personality in a polar seabird

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“In all these things, there is much evidence that the mind of a bird works according to the individual as well as to the species.”

– Len Howard, Birds as Individuals

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Abstract

Individual animals differ in how they behave. One of the best-studied manifestations of this is foraging behaviour: individuals of many species specialise their feeding to varying degrees, some being highly site faithful and consistent in their foraging strategies, while others are not. Individual variation in foraging can have important fitness implications, including via carry-over effects, whereby an individual's condition in one season can influence its performance in future seasons. Understanding individual variation in foraging behaviour therefore constitutes a fundamental goal in ecological research. Recent studies indicate that animal personality – consistent individual variation in fundamental behavioural traits, e.g. boldness, or aggression – may lead individuals to differ in their foraging behaviour and how resources are allocated to breeding. This suggests that personality may explain how specialised individuals are in their foraging behaviour, and how individuals are impacted by carry-over effects. Seabirds represent model species to test these predictions: owing to the relative ease with which they can be tracked, individual variation in foraging movements and behaviours are known to be highly prevalent in seabirds. Furthermore, their vulnerability to environmental change, particularly in the polar regions, means that understanding seabird foraging behaviours and breeding performance is highly pertinent. In this thesis, I focus on the behaviour of black-legged kittiwakes (*Rissa tridactyla*) from five breeding colonies in the High Arctic archipelago of Svalbard. I used two types of biologging device – GPS loggers and geolocator-immersion loggers – to examine individuals' foraging behaviour during both the breeding season, when kittiwakes are central-place foragers, and the non-breeding season, when kittiwakes migrate to the West Atlantic and overwinter at sea. I also conducted repeat behavioural tests on breeding individuals over two years, revealing that kittiwakes exhibit highly repeatable individual variation in boldness. Firstly, I demonstrate that bolder kittiwakes are more faithful to foraging sites and more repeatable in their foraging trips than shy individuals during the breeding season. Secondly, by applying a resource selection function approach, I further show that bolder kittiwakes are also more consistent in their habitat preferences, and forage preferentially in deeper waters than shy individuals, potentially reflecting a greater usage of predictable habitat features. Finally, I show that despite exhibiting similar levels of foraging activity during the non-breeding season, bold and shy kittiwakes differ in

how their non-breeding foraging carries over to impact subsequent breeding performance, potentially reflecting differences in resource allocation trade-offs. The results of this thesis provide novel explanations for previously unexplained variation in foraging behaviour, which is known to be taxonomically widespread, suggesting relevance extending beyond kittiwakes and seabirds to other species. Furthermore, these results provide new evidence to support the growing consensus that personality is linked to the consistency of behaviour, with important implications under environmental change scenarios. Collectively, the work in this thesis highlights the importance of personality as a fundamental trait with the potential to explain broader and more complex patterns of behaviour observed in animal populations.

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Chapter 1

General introduction

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General Introduction

The foraging behaviour of individual animals

An organism's potential to survive and reproduce is conditional on its ability to acquire food resources. A spectacularly diverse array of solutions to this fundamental requirement have evolved at all levels of the animal kingdom: broad animal groups vary widely in the food types they consume (e.g. carnivores, herbivores, omnivores); at a finer scale, different species adopt distinct strategies to acquire their resources, such as the sit-and-wait tactic of ambush predators, or the chase-driven hunt of pursuit predators.

Over recent decades, ecologists have increasingly recognised that individual animals also show substantial variation in their foraging behaviour. This constitutes an important conceptual departure from earlier foraging theory: the foraging niche – a term encompassing an animal's resource use, foraging behaviour, and foraging habitat (Stephens *et al.*, 1986) – was historically regarded as a property of species or populations, and individuals within populations were typically viewed as ecologically identical. Furthermore, attempts to explain animals' foraging decisions have traditionally relied upon optimal foraging theory, which broadly predicts that animals should adaptively modify their behaviour to the prevailing conditions in order to maximise their intake rate at minimal cost (MacArthur *et al.*, 1966; Stephens *et al.*, 1986). Consequently, an individual animal's foraging behaviour was considered to be highly plastic and adjustable. However, it is now known that individuals within populations often vary greatly from one another in their foraging niche, and exhibit high levels of consistency in their foraging behaviour over time (Figure 1.1; Roughgarden, 1972; Bolnick *et al.*, 2003; Phillips *et al.*, 2017). When individuals use different subsets of the population-level foraging niche for reasons not attributable to their age, sex, or discrete morphological group, this phenomenon is referred to as individual foraging specialisation (Bolnick *et al.*, 2003; Araújo *et al.*, 2011). Individual specialisation is often accompanied by behavioural consistency, although while consistency often reflects specialisation, the two are not equivalent (Cleasby *et al.*, 2015; Carneiro *et al.*, 2017). Consistency describes low within-individual variation, but not necessarily relative to the variation that exists at the population level (Bolnick *et al.*, 2003).

Individual variation in foraging behaviour is now documented in all major animal taxa (reviewed by Bolnick *et al.* 2003; Araújo *et al.* 2011), with niche differences among individuals sometimes exceeding those among species (e.g. Ehlinger & Wilson 1988; Meyer 1989). Such individual differences are thought to be adaptive because they limit niche overlap, and, therefore, intraspecific resource competition (Van Valen, 1965; Roughgarden, 1972; Svanbäck *et al.*, 2007; Huss *et al.*, 2008; Araújo *et al.*, 2011). The implications of individual specialisation are profound and far-reaching. Differences in foraging niche can influence individuals' foraging efficiency, reproductive success, and survival (Laverty *et al.*, 1988; Bolnick *et al.*, 2003; Cucherousset *et al.*, 2011; Terraube *et al.*, 2011; Potier *et al.*, 2015). Meanwhile, specialised foraging implies constraints on individuals' ability to respond to changes in their environment (i.e. behavioural plasticity: Dingemanse *et al.*, 2010; DeWitt *et al.*, 1998). These individual consequences can scale up to influence population dynamics (Dall *et al.*, 2012). While specialised foraging may restrict an individual's plasticity, populations comprised of behaviourally differentiated individuals may be better buffered against the impacts of resource shifts, because individuals should respond non-uniformly (Bolnick *et al.*, 2003; Tinker *et al.*, 2008). Understanding individual differences in foraging behaviour is thus crucial to accurately predicting and managing population responses to environmental change.

As well as differing in their foraging niche, individuals within populations may differ in niche width, i.e. the degree to which they are specialised (Figure 1.1c), with specialists and generalists coexisting within populations (Wilson *et al.*, 1994; Svanbäck *et al.*, 2004; Catry *et al.*, 2014). For example, after experimental introduction of bluegill sunfish (*Lepomis macrochirus*) into a new pond, individuals quickly divide into benthic specialists, limnetic specialists, or generalist foragers, utilising both resource types (Werner *et al.*, 1981). Variation in the degree to which animals are specialised in their foraging behaviour is particularly interesting because generalists display the variability we would predict to be adaptive in dynamic environments (DeWitt *et al.*, 1998; Reed *et al.*, 2010). However, there often appear to be costs associated with generalist strategies, such as reduced foraging performance compared to foraging specialists (e.g. Laverty & Plowright 1988), a concept referred to as the "jack-all-all-trades, master-of-none" hypothesis (Rosenzweig 1981). While being a generalist may confer benefits in

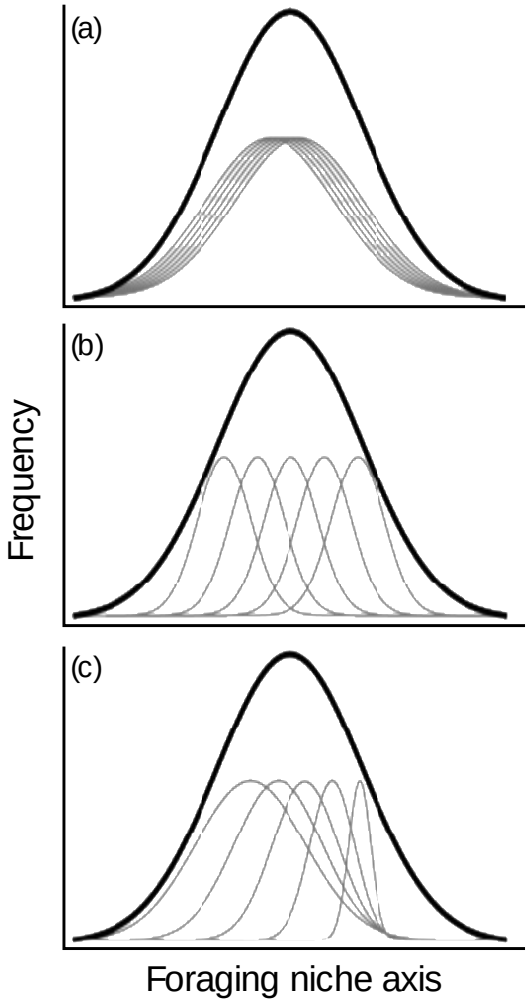

Figure 1.1. Schematic adapted from Bolnick *et al.* (2003) showing how the population-level foraging niche (thick curves) is comprised of the foraging niches of its individuals (thin curves). In scenario (a), all individuals are foraging generalists, each utilising most of the population niche; in scenario (b), all individuals are foraging specialists, each utilising a narrow subset of the population niche and minimising overlap with others; in scenario (c), individuals vary on a spectrum of generalist to specialist foraging strategies, with niche width different for each individual.

unpredictable environments, stable conditions often favour specialists (Wilson *et al.*, 1994; van de Pol *et al.*, 2010). The drivers of variation in niche and niche width are, however, not well known, despite the clear consequences of such variation for population dynamics in a changing world (Bolnick *et al.*, 2003).

Foraging movements and space use

Movement is key to foraging: very few animals are able to acquire resources without some form of movement. Just as individual animals may show consistent differences in their diets, individuals may also be highly specialised in their foraging movements and space use (Carneiro *et al.*, 2017; Shaw, 2020). Over the past decade, innovations in animal tracking have greatly bolstered the study of individual movement specialisation, and the field is now burgeoning. A growing range of biologgers, including GPS loggers, light-level geolocators, time-depth recorders, and radio transmitters, are available at increasingly smaller sizes, permitting the remote recording of foraging movements in free-ranging animals from butterflies to blue whales (e.g. Kissling *et al.* 2014; Abrahms *et al.* 2019). Such tracking data have revealed that many species show individual foraging site fidelity, whereby individuals repeatedly return to the same locations to forage, and in doing so spatially segregate from others in their population (e.g. in bats: Kerth *et al.* 2001; in fur seals: Baylis *et al.* 2012; in seabirds: Patrick *et al.* 2014; in bumblebees: Woodgate *et al.* 2016; in sea turtles: Shimada *et al.* 2020). In addition to site fidelity, individuals may show consistency in the spatial characteristics of foraging trips, such as the range, distance or direction in which they travel to forage (Hamer *et al.*, 2001; Patrick *et al.*, 2014; Potier *et al.*, 2015), and consistent use of particular habitat types (Lowther *et al.*, 2011; Wakefield *et al.*, 2015; Leclerc *et al.*, 2016).

Individual specialisation and consistency in foraging movements are particularly prevalent in marine predators such as seabirds, pinnipeds, and cetaceans (Ceia *et al.*, 2015; Carneiro *et al.*, 2017; Phillips *et al.*, 2017). Tracking studies have revealed that marine predators often show consistent individual differences in their use of foraging sites (Patrick *et al.*, 2014; Arthur *et al.*, 2015; Wakefield *et al.*, 2015), habitat preferences (Ropert-Coudert *et al.*, 2003; Lowther *et al.*, 2011), foraging trips characteristics (e.g. outward bearing, path straightness; Hamer *et al.* 2001; Patrick *et al.* 2014; Potier *et al.* 2015), and prey capture techniques (Hoelzel *et al.*, 1989; Kato *et al.*, 2000). Specialisation in foraging movements is thought to be favoured by the distribution of resources in the marine environment: prey resources tend to be patchily distributed at sea, and relatively predictable over timescales of days to weeks (Weimerskirch, 2007; Fauchald, 2009). Under such conditions, individuals are likely to benefit from familiarity gained by consistent use of foraging sites, routes and habitats (Switzer, 1993; Wolf *et al.*, 2009),

promoting the emergence of specialised foraging. Furthermore, when breeding, many marine predators (and notably seabirds) are central-place foragers, i.e. constrained to depart from and regularly return to a common location, such as a breeding colony or communal roost. Central-place foraging is also associated with high levels of individual specialisation in foraging movements (e.g. Kerth *et al.* 2001; Arthur *et al.* 2015; Ceia & Ramos 2015; Woodgate *et al.* 2016; Carneiro *et al.* 2017; Phillips *et al.* 2017), as intense intraspecific resource competition favours the partitioning of foraging locations and strategies (Villegas-Amtmann *et al.*, 2008; Patrick *et al.*, 2014; Sheppard *et al.*, 2018). While the predictable resource distributions experienced by centrally constrained marine predators provide mechanisms for the emergence of individual specialisation, we often still lack an understanding of the factors shaping individual niches. In other words, when a group of individuals, each starting from the same central location, share equal access to the same foraging landscape, what factors shape each individual's foraging behaviour? Addressing this question is key to developing a mechanistic understanding of individual foraging and movement (Bolnick *et al.*, 2003; Nathan *et al.*, 2008).

Factors determining individuals' foraging behaviour

An individual's foraging behaviour will vary as a function of aspects of its phenotype because of morphological, physiological and behavioural differences in foraging capabilities and requirements (Bolnick *et al.*, 2003). Animals of different sexes or age classes often show characteristic differences in foraging movements, arising from the effects of sexual dimorphism (Gonzalez-Solis *et al.*, 2000; Phillips *et al.*, 2004), sex differences in breeding roles (Pinet *et al.*, 2012; Hedd *et al.*, 2014), or age-related variation in foraging experience (Votier *et al.*, 2017; Grecian *et al.*, 2018). However, individual specialisation is usually defined as the residual individual variation unexplained by sex and age differences (Bolnick *et al.*, 2003). Individual morphological (e.g. van de Pol *et al.* 2010), and physiological differences (e.g. Watanabe 2006) have also been shown to be important factors shaping animals' foraging behaviour. However, the contribution of individual behavioural variation, or animal personality, has received

markedly less attention, a surprising omission given the commonalities between the two fields of research.

Animal personality (sometimes also referred to as temperament) refers to individual differences, consistent over time and across contexts, in fundamental behavioural traits. Typically, these traits are organised into five major axes: (1) boldness, how an animal responds to risk; (2) aggressiveness, an animal's tendency to agonistic reactions towards conspecifics; (3) activity, the level of active behaviour an animal shows in a familiar environment; (4) exploration, an animal's reaction to a new scenario; (5) sociability, an animal's (non-aggressive) response to the presence of conspecifics (Réale *et al.*, 2007). Often, these personality axes are correlated into suites of behavioural traits, or "behavioural syndromes" (Sih *et al.*, 2004); for example, funnel web spiders *Agelenopsis aperta* that exhibit bolder responses to an emergence test (are faster to re-emerge from their funnel following a simulated predation attempt) are also more aggressive towards conspecifics (Riechert *et al.*, 1993). Research into animal personality has surged over the past two decades, revealing a taxonomically ubiquitous phenomenon whereby within-individual variation in these traits is surprisingly low (Gosling, 2001; Réale *et al.*, 2007; Bell *et al.*, 2009), and it is becoming clear that personality variation has major implications for evolutionary and ecological processes (Sih *et al.*, 2004, 2012; Réale *et al.*, 2007).

Differences in personality among individuals are likely to influence foraging behaviours, and particularly foraging movements, for a variety of reasons (Toscano *et al.*, 2016; Spiegel *et al.*, 2017). Fundamentally, the methods used by researchers to assay personality traits often directly measure animals' movement tendencies (e.g. activity, exploration). Even the bold-shy axis, which captures how an animal responds to risk, is often measured as the propensity to move into or away from a risky situation (e.g. latency to emerge into a novel environment, Schirmer *et al.* 2019; response to a novel object, Dammhahn 2012). In a broader ecological context, such a trait may explain differences between animals in the tendency to forage in open versus sheltered habitat (e.g. Ciuti *et al.* 2012). Much of the individual variation observed in animals' foraging movements may thus directly capture variation in animal personality (Nilsson *et al.*, 2014).

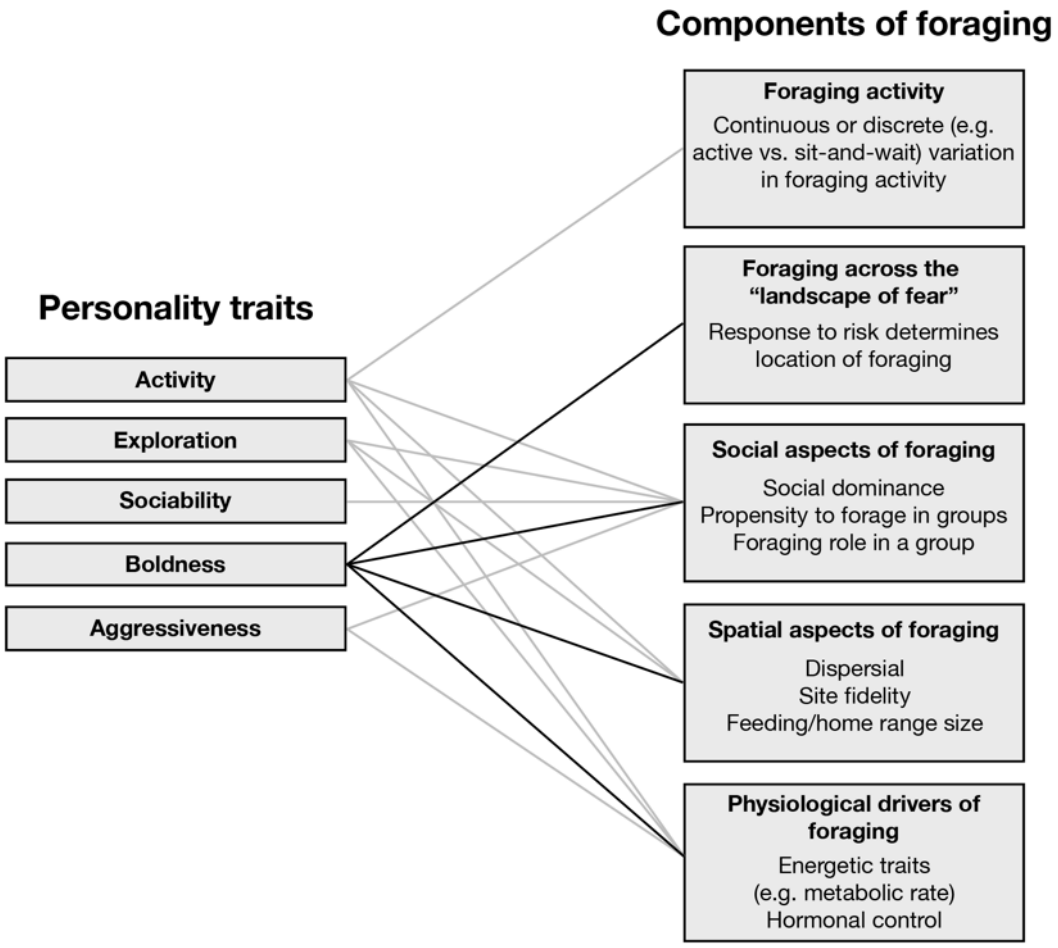

Figure 1.2. A conceptual framework adapted from Toscano *et al.* (2016) linking animal personality axes to aspects of consumer foraging behaviour. Links are supported by studies listed in Table 1 of Toscano *et al.* (2016). Links between components of foraging and boldness (the personality axis examined in this thesis) are in black.

Beyond methodological associations, personality traits have the potential to influence foraging behaviour via links to other aspects of individuals' behaviour and ecology (outlined in Figure 1.2). Specifically, Araújo *et al.* (2011) predicts three ways by which individual variation, such as in personality traits, may drive differences in foraging. Firstly, personality may lead individuals to have different preferences for particular diets or foraging habitats. For instance, personality may influence individual's ability to detect, acquire, or digest particular food types (e.g. Bijleveld *et al.*, 2014; Chang *et al.*, 2017; Serrano-Davies *et al.*, 2017), or their energetic requirements (Careau *et al.*, 2008), such that individuals differ in the resources (and by extension foraging habitats and behaviours) they would optimally prefer. Secondly, personality may influence an individual's decisions in trade-offs that arise when foraging for their preferred

resources. For example, shy individuals may be expected to make foraging decisions which minimise predation risk, whereas bold individuals should maximise resource gain (e.g. Quinn *et al.*, 2012), and these different optimisation criteria may lead individuals to make different foraging decisions based upon their personality. Thirdly, personality is likely to influence an individual's foraging decisions in the context of ecological interactions. For example, bold individuals may be of a higher competitive ability and thus dominate in foraging scenarios (Pintor *et al.*, 2008; Webster *et al.*, 2009), or otherwise occupy larger territories or home ranges (Spiegel *et al.*, 2017; Schirmer *et al.*, 2019), and thus restrict shy individuals' ability to acquire their preferred resources.

Collectively, these factors suggest that personality has high potential to explain widespread individual variation in foraging behaviour, and indeed a growing body of research supports this (reviewed in Toscano *et al.*, 2016). However, most studies examine only the link between personality and average-level foraging differences, such as the mean distance an animal travels to forage (Patrick & Weimerskirch, 2014), or the average depth it dives to (Traisnel *et al.*, 2019). As the growing number of studies on individual foraging behaviour demonstrates, individual variation in foraging behaviour is more complex than can be summarised in mean-level individual differences: individuals also vary in the consistency and variability they show in their foraging behaviour, such as their site fidelity (e.g. Wakefield *et al.*, 2015). The potential for personality to explain individual variation of this sort is underexplored.

Fitness consequences of individual differences in personality and foraging behaviour

Because foraging is the means by which animals acquire the resources required to reproduce, individual variation in foraging behaviour is often associated with differences in breeding performance (Lemon, 1991; Golet *et al.*, 2000; Votier *et al.*, 2004; Vander Zanden *et al.*, 2014). Variation in personality traits, too, often carry fitness consequences (Smith *et al.*, 2008), but the mechanistic links by which personality traits lead to fitness differences are often not described. Personality-dependent foraging behaviour represents an important, yet under-explored, pathway by which personality may be

connected to fitness. For example, a number of studies link personality traits to fitness consequences which fluctuate with changes in resource availability over time (Dingemanse *et al.*, 2004; Boon *et al.*, 2007); but how personality interacts with resource availability to determine fitness is not fully resolved.

The fitness consequences of foraging behaviour may not always be immediately detectable, but may be lagged over time. A growing body of research has demonstrated the phenomenon of carry-over effects on breeding, whereby events and processes prior to breeding drive an animal's current reproductive performance (Harrison *et al.*, 2011). Carry-over effects are thought to arise when animals fail to acquire sufficient resources during the non-breeding season to prepare them for the energetic demands of the breeding season. Accordingly, carry-over effects of variation in individuals' diet, foraging behaviour, and foraging habitat during the non-breeding period are frequently detected (Norris *et al.*, 2004; Kennedy *et al.*, 2008; Sorensen *et al.*, 2009; Daunt *et al.*, 2014). Carry-over effects have been documented in many species (in turtles: Broderick *et al.* 2001; in whales: Perryman *et al.* 2002; in fish: Kennedy *et al.* 2008; in *Drosophila* sp: Betini *et al.* 2013; in songbirds: Montreuil-Spencer *et al.* 2019), including seabirds, facilitated by the relative ease with which seabird individuals can be tracked across multiple breeding and non-breeding seasons. The occurrence and strength of carry-over effects often varies greatly (e.g. Daunt *et al.* 2014), but few studies attempt to explain the causes of this variation.

No study has yet examined the role of personality in shaping carry-over effects. Yet, it is likely that personality drives individual differences in foraging behaviour outside of the breeding period (as previously demonstrated during the breeding season), and that these differences carry-over to affect subsequent breeding performance. Furthermore, life-history theory predicts that personality should influence individuals' allocation to self-maintenance versus reproductive effort (Biro *et al.*, 2008; Réale *et al.*, 2010), implying that individuals varying in personality may differ in their response to non-breeding conditions. Through the use of biologging devices, carried by animals between breeding seasons, tools now exist to test this prediction, and address how foraging conditions interact with life history strategies to drive individual heterogeneity in reproductive performance.

Seabirds as a model system

Seabirds provide excellent models to examine the links between individual foraging behaviour and personality. Seabirds are typically apex predators, ranging widely in their foraging movements to locate patchily distributed prey (Weimerskirch, 2007; Fauchald, 2009), and during the breeding season are constrained to return regularly to their nest sites. Many species are large enough to carry biologging devices, both during and outside of breeding seasons, facilitating the tracking of individuals' year-round foraging behaviour. From the wealth of seabird tracking data produced by biologging studies in recent years, the incidence of individual foraging specialisations has been shown to be very high in this taxa (Ceia *et al.*, 2015; Carneiro *et al.*, 2017; Phillips *et al.*, 2017), warranting an understanding of the proximate drivers of individual variation in foraging behaviour.

Studies examining personality traits in seabird species have been comparatively scarce, although recent years have seen these gain traction (e.g. Patrick & Weimerskirch, 2013; Grace & Anderson 2014; Patrick & Weimerskirch, 2014; Collins *et al.* 2019; Traisnel & Pichegru 2019). Personality traits have been linked to individual foraging movements (Patrick & Weimerskirch, 2014), position in foraging trade-offs (Patrick *et al.*, 2017), and dive patterns (Traisnel *et al.*, 2019) in breeding seabirds, with consequences for individual fitness (Patrick & Weimerskirch, 2014; Patrick *et al.*, 2015). Studies are yet to address links between personality and foraging niche width, or foraging outside the breeding season.

Study species: the black-legged kittiwake

Black-legged kittiwakes (*Rissa tridactyla*; hereafter "kittiwakes") are small, sexually monomorphic, colonial gulls with a circumpolar breeding distribution in the northern hemisphere. Of all 100+ species in the family Laridae, kittiwakes are the most pelagic, spending their lives almost exclusively at sea (Coulson, 2011). The exception to this is during the breeding season, when they breed on the ledges of coastal cliffs, and increasingly, on anthropogenic structures such as buildings.

The breeding season commences when kittiwakes return to the colony in spring, with males occupying nest sites first. Partner fidelity from one year to the next has been recorded at around 70%, with death of one partner accounting for around 50% of instances when pairs separate (Hatch *et al.*, 1993). Kittiwakes are socially monogamous, and the rate of extra-pair fertilisation is low (Helfenstein *et al.*, 2004). After re-forming a partnership or beginning a new one, the pair initially spend much time engaging in courtship displays and activity, before beginning nest building together (Coulson, 2011). Nest structures are cup-shaped and build from mud and vegetation, often on top of the remains of the previous year's nest (Coulson, 2011). The duration of the nest building period is highly variable, with some pairs spending several weeks on the task, while others (typically late-arriving birds) spending only 3-4 days. The timing of breeding within a colony and within a year is fairly asynchronous, with hatching known to occur over a period of two weeks (Descamps, 2019).

Kittiwakes lay a single clutch per year, with clutches consisting of one to three eggs, but usually two (Coulson & White, 1957). The incubation period last around 27 days, and the fledging period around 40 days, with both parents sharing the roles of incubation and chick provisioning (Coulson & White, 1957; Coulson, 2011). After fledging, chicks may return to the nest to be fed by their parents for a brief period, and finally depart the colony around ten days after their first flight (Coulson, 2011). Natal philopatry is fairly high (around 30%; Danchin & Monnat, 1992), and recruits begin to return to the colony to breed from around 3-5 years of age, (Coulson, 2011). Individuals can breed for more than 10 years after recruitment (Danchin & Monnat, 1992). Average life expectancy is estimated at 13 years (Hatch *et al.*, 1993), although adult kittiwakes may reach 20 years of age (Elliott *et al.*, 2014). Annual adult survival is low, with most mortality occurring away from the breeding colony during winter (Aebischer & Coulson, 1990; Hatch *et al.*, 1993). Adult mortality is predominantly thought to be due to starvation (Coulson, 2011), but predation of adults by skuas is known (Heubeck *et al.*, 1999).

Kittiwakes breed on an annual basis. but a proportion of adults skip breeding in any given year, often following poor foraging conditions in the preceding winter (Danchin *et al.*, 2002; Goutte *et al.*, 2010). The probability of breeding deferral is higher among inexperienced breeders than experienced birds (Desprez *et al.*, 2011), and inexperienced

birds have lower breeding success on average (Aubry *et al.*, 2009). Breeding performance can be highly variable among individuals within kittiwake colonies (Steiner *et al.*, 2010; Coulson, 2011), while variation in productivity between colonies is closely linked to prey abundance and environmental conditions (Harris *et al.*, 1990; Suryan *et al.*, 2002; Frederiksen *et al.*, 2005, 2007). Significant declines in the global kittiwake population, thought to be linked to their sensitivity to changing conditions, have led to its evaluation as a "vulnerable" species in 2017 (BirdLife International, 2019).

Kittiwakes are among the best-studied of seabird species, particularly in terms of their foraging behaviour. Kittiwakes are obligate surface-feeders, capturing small fish and marine invertebrate prey whilst sitting on the sea surface, or by shallow dives (<1m) from the air. As with many seabird species, during the breeding season kittiwakes are constrained in the duration (and therefore distance) of their foraging trips by the needs of both their nest-attending partner and, post-hatching, their chicks. Despite these constraints, kittiwakes can travel impressively far from the colony while breeding: Christensen-Dalsgaard *et al.*, (2018) reported that the average foraging trip made by chick-rearing kittiwakes at the Norwegian colony of Sør-Gjæslingan covers almost 800km. Kittiwakes tend to forage further still from the colony prior to hatching, during incubation (Robertson *et al.*, 2014): typical of many other seabird species, kittiwakes tend to make more frequent returns to the colony during chick rearing (Daunt *et al.*, 2002).

Outside of the breeding season, kittiwakes spend their lives at sea. During this period, Arctic-breeding kittiwakes – along with most of the rest of the Atlantic kittiwake population – migrate to the West Atlantic, wintering between Newfoundland and the Mid-Atlantic Ridge (Frederiksen *et al.*, 2012). Research has found that the timings of migratory movements are linked to past and future reproductive success, suggesting a complex pattern of interacting carry-over effects: kittiwakes experiencing reproductive failure in a given year depart the colony earlier (Bogdanova *et al.*, 2011) and stay longer at their wintering grounds (Bogdanova *et al.*, 2017). Late return to the breeding colony then predicts poorer breeding success the subsequent spring (Bogdanova *et al.*, 2017). While the mechanisms underpinning these relationships are not fully resolved, physiology is thought to play an important role, namely the primary avian stress

hormone corticosterone (Schultner *et al.*, 2014). Environmental conditions experienced during the winter also play a role in determining subsequent breeding performance for kittiwakes. Frederiksen et al. (2007) reported a negative relationship between productivity of British kittiwake colonies and sea surface temperature (SST) in the preceding winter, likely due to the concomitant negative relationship between SST and abundance of sandeel (*Ammodytes spp.*; the principal prey item of kittiwakes breeding in Britain). These patterns indicate the importance of efficient foraging even outside of the breeding season for subsequent successful breeding in this species.

Kittiwakes are particularly vulnerable to changes in prey availability (Monaghan *et al.*, 1996; Furness *et al.*, 2000), as they are reliant upon prey at the sea surface, and so are unable to access prey deeper in the water column. As a result, their foraging behaviour can often be linked to environmental factors that shape the distribution of prey at the ocean's surface: kittiwakes are often observed foraging in areas of ocean temperature gradients (Robertson *et al.*, 2014; Wakefield *et al.*, 2017), along continental shelf breaks or seamounts (Burger *et al.*, 2004; Christensen-Dalsgaard *et al.*, 2018), and in the Arctic, at tidewater glacier fronts (Urbanski *et al.*, 2017). With such a wealth of information indicating foraging opportunities, it is unsurprising that even within colonies, individual kittiwakes show highly variable foraging strategies, making both coastal and pelagic trips (Christensen-Dalsgaard *et al.*, 2018), highly variable in distance and range (Suryan *et al.*, 2000), and showing both high and low fidelity to foraging sites (Irons, 1998). This variation in foraging behaviour, and obvious links with fitness, make kittiwakes ideal candidates for studying individuality in behaviour, foraging, and life-history.

Study sites

In this thesis, I examine the links between individual personality and foraging behaviour, across the annual cycle, in kittiwakes breeding on the island of Spitsbergen, in Svalbard. The archipelago of Svalbard is situated in the High Arctic in the Barents Sea. Svalbard's wildlife is experiencing rapid and dramatic environmental change, as glaciers retreat, sea-ice shrinks, and temperatures rise at three times the global rate (Comiso *et al.*, 2014). These physical changes are resulting in the Atlantification of Svalbard's marine

ecosystems, including by range expansions of boreal species, influencing the entire food web (Descamps *et al.*, 2017). The process can be observed in the shifts in diet of Svalbard's kittiwakes, from predominantly Arctic prey such as polar cod (*Boreogadus saida*), to increasing proportions of Atlantic prey, such as Atlantic herring (*Clupea harengus*) and Atlantic cod (*Gadus morhua*; Vihtakari et al., 2018).

Approximately 270,000 pairs of kittiwakes breed in Svalbard (Norwegian Polar Institute, 2020). The foraging behaviour of Arctic-breeding kittiwakes appears to differ from kittiwakes in the rest of the Atlantic in a number of ways. Firstly, as already mentioned, dietary samples from Svalbard kittiwakes reveal much broader range of prey consumed than the predominantly sandeel-consuming British kittiwakes. Polar cod dominate, along with capelin (*Mallotus villosus*), herring, amphipods, krill, and shrimp, while other groups including polychaetes, gastropods and cephalopods are also known (Vihtakari *et al.*, 2018). This broad dietary niche contrasts with reports of a more limited selection of prey by kittiwakes in the Atlantic (Furness *et al.*, 2000; Coulson, 2011). Secondly, tidewater glacier fronts emerge as an important habitat type for kittiwakes feeding in Arctic waters. During the summer months, freshwater discharged from melting glaciers generates upwellings of marine invertebrates paralysed by osmotic shock, producing prey-dense hotspots for vertebrate predators (Węsławski & Legezytńska, 1998; Węsławski *et al.,* 2000). Kittiwakes have long been recorded to congregate and feed at glacier fronts, often in groups of thousands of individuals (Hartley *et al.*, 1936), and the relative importance of glacier fronts as foraging habitat for marine predators may increase as other foraging habitat deteriorates faster in the Arctic (Lydersen *et al.*, 2014). Understanding how kittiwakes use the resources available to them has never been more important.

There are around 215 known kittiwake colonies in Svalbard (Norwegian Polar Institute, 2020), where kittiwakes breed on sea cliffs, but also on disused buildings, such as those remaining in a number of abandoned mining towns located around Spitsbergen. The accessibility of such colonies presents a unique opportunity for access to Arctic-breeding seabirds and greatly facilitates their close study. For the present thesis, I gathered behavioural data on kittiwakes breeding at both cliff-based and building-based colonies at three main sites on the west coast of Spitsbergen (Figure 1.3):

Grumantbyen – all data chapters presented in this thesis use behavioural data collected on kittiwakes breeding at Grumantbyen (78°10'N, 15°05'E). Grumantbyen (also shortened to Grumant) is a former mining settlement in Isfjorden consisting of several abandoned buildings, one of which has been colonised on the sea-facing side by kittiwakes. Approximately 45 kittiwake pairs breed there each year.

The Kongsfjorden colonies – data was also collected at three cliff-based kittiwake colonies for inclusion this thesis. Blomstrand (78°59'N, 12°07'E; 900 breeding pairs), Krykkjefjellet (78°53'N, 12°11'E; 200 breeding pairs), and Observasjonholmen (78°56'N, 12°16'E; 150 breeding pairs) are situated in close proximity to one another in the inlet of Kongsfjorden. Two tidewater glacier fronts at the head of Kongsfjord constitute important foraging areas for seabirds in the area.

Pyramiden – this thesis also includes data collected from kittiwakes breeding at a large abandoned Russian mining settlement, Pyramiden (78°39'N, 16°19'E). Over 1,000 kittiwake pairs breed on a number of disused buildings at Pyramiden each year. In 2018, I established a study site in Pyramiden with Samantha Patrick for further research into the individual behaviour of Arctic kittiwakes. Behavioural data from Pyramiden features in one chapter of this thesis.

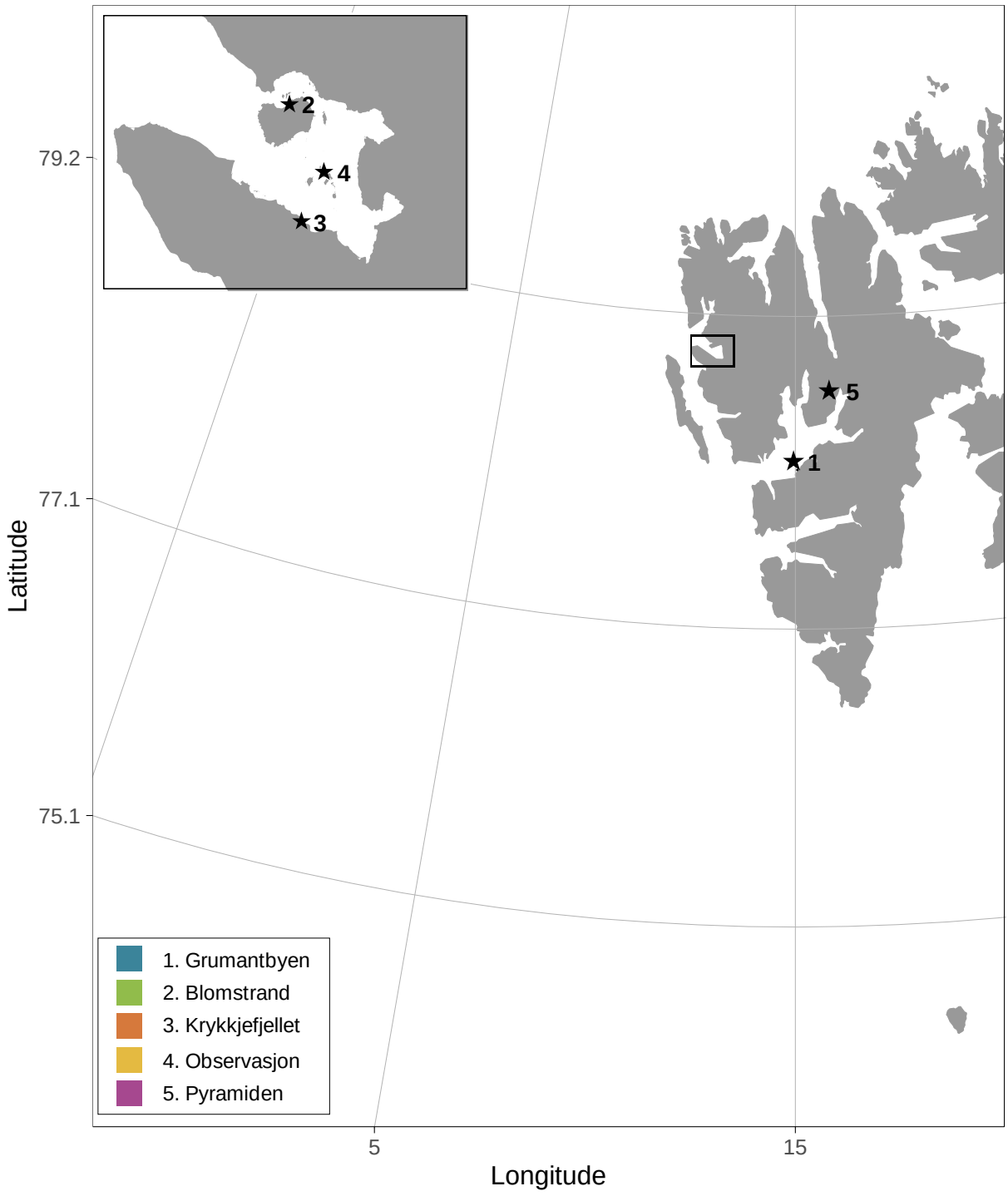

Figure 1.3. The locations of breeding colonies in Svalbard from which kittiwakes were studied for this thesis, with GPS tracks of all foraging trips used in analysis of breeding season foraging behaviour (Chapters 2 and 3). Birds were tracked in 2017 and 2018. Chapter 2 uses data from Grumantbyen, Blomstrand, Krykkjefjellet, and Observasjonholmen collected in 2017, while Chapter 3 uses data from all five colonies and from both years. Map created in the PlotSvalbard package (Vihtakari 2019).

Thesis aims and outline

The overarching aim of this thesis is to understand the relationship between personality and individual foraging behaviour, and the associated life-history consequences, in an Arctic seabird. By incorporating data from GPS loggers during the breeding season and geolocator immersion loggers during the non-breeding season, I explore the links between personality and year-round foraging behaviour in kittiwakes. I examine their fine-scale foraging movements and habitat selection during the breeding season, in order to test a number of previously untested hypotheses relating to personality, space use, and movement behaviour. Further, I then investigate the fitness consequences of interactions between personality and winter foraging behaviour, with aims of better understanding the intrinsic drivers of carry-over effects. While this thesis focusses on kittiwakes, the implications of the results presented here extend beyond seabirds to provide a greater understanding of the intrinsic drivers of movement behaviour, and the complex relationships between individual behavioural variation and fitness.

In **Chapter two**, I explore the links between boldness, the best-studied personality trait, and foraging movement specialisation. Using GPS tracking data from kittiwakes breeding at four colonies, I test the hypothesis that boldness will relate to the consistency and degree of specialisation individuals show in their spatial foraging behaviour. I use multiple analytical approaches to quantify foraging variation, including repeatability analysis and a similarity index to measure individual foraging site fidelity.

- Chapter published: Harris SM, Descamps S, Sneddon LU, Bertrand P, Chastel O, Patrick SC (2020) Personality predicts foraging site fidelity and trip repeatability in a marine predator. *Journal of Animal Ecology*, **89** (1): 68-79.

Chapter three builds on the findings of a link between boldness and spatial consistency in chapter two, and asks whether this link is driven by personality-dependent habitat selection. I quantify variation in habitat selection in relation to four key environmental drivers of foraging habitat for kittiwakes using a resource selection function approach, and then examine the link between personality and habitat selection. I predict that personality would be linked to (i) individual differences in habitat preference, and (ii)

differences in the consistency of habitat selection. This chapter uses data collected over two years from five kittiwake colonies.

- Chapter in preparation for submission: Harris SM, Bertrand P, Descamps S, Sneddon LU, Trevail AM, Chastel O, Strøm H, Patrick SC. Does personality predict individual habitat selection in a marine predator?

In **Chapter four**, my focus shifts from examining foraging during the breeding season to non-breeding foraging activity, and its links to personality. I test for a carry-over effect of winter foraging behaviour on subsequent breeding performance, and that variation in the magnitude of this effect will correlate with personality, reflecting individual differences in pace-of-life. This study uses data from Grumantbyen only, and includes historical tracking data to give a dataset spanning six years from 2013-2018.

- Chapter awaiting decision from *Proceedings of the Royal Society B* after undergoing revisions (May 2020): Harris SM, Descamps S, Sneddon LU, Cairo, M, Bertrand P, Patrick SC. Personality-specific carry-over effects on breeding.

Finally, in **Chapter five**, I summarise the key findings of the chapters above and synthesise these results in the broader context of animal behaviour and foraging ecology. I discuss implications of these findings, and outline ideas for future directions.

A note on the text

Chapters 2 – 4 of this thesis have been written as stand-alone papers for submission to peer-reviewed journals. They are tied by the common link of individual variation in foraging behaviour and personality in kittiwakes. Only minor alternations have been made to these chapters to improve the readability and cohesiveness of this thesis, and therefore some information is repeated across chapters.

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Chapter 2

Personality predicts foraging site fidelity and trip repeatability in a marine predator

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Personality predicts foraging site fidelity and trip repeatability in a marine predator

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Abstract

Animal populations are often comprised of both foraging specialists and generalists. For instance, some individuals show higher foraging site fidelity (spatial specialisation) than others. Such individual differences in degree of specialisation can persist over timescales of months or even years in long-lived animals, but the mechanisms leading to these different individual strategies are not fully understood. Meanwhile, there is accumulating evidence that individual variation in foraging behaviour is shaped by animal personality traits, such as boldness. Despite this, the potential for boldness to drive differences in the degree of specialisation is unknown. In this study, we used novel object tests to measure boldness in black-legged kittiwakes (*Rissa tridactyla*) breeding at four colonies in Svalbard, and deployed GPS loggers to examine their at-sea foraging behaviour. We estimated the repeatability of foraging trips, and used a hidden Markov model to identify locations of foraging sites in order to quantify individual foraging site fidelity. Across the breeding season, bolder birds were more repeatable than shy individuals in the distance and range of their foraging trips, and during the incubation period (but not chick rearing), bolder individuals were more site faithful. Birds exhibited these differences while showing high spatial similarity in foraging areas, indicating that site selection was not driven by personality-dependent spatial partitioning. We instead suggest that a relationship between boldness and site fidelity may be driven by differences in behavioural flexibility between bold and shy individuals. Together, these results provide a potential mechanism by which widely reported individual differences in foraging specialisation may emerge.

Keywords: biologging; boldness; foraging niche width; foraging specialisation; marine vertebrate; movement ecology; personality; site fidelity

1.0 Introduction

Among individual differences often comprise the majority of a population's variation in behaviour (Bolnick *et al.*, 2003; Araújo *et al.*, 2011; Dall *et al.*, 2012). Individual foraging specialisations are a particularly widespread example, whereby individuals utilise only a subset of the population foraging niche (Bolnick *et al.*, 2003). Foraging site fidelity is a

common type of behavioural specialisation whereby individuals show spatial consistency in their foraging behaviour, repeatedly visiting the same locations (Hillen *et al.*, 2009; Baylis *et al.*, 2012; Wakefield *et al.*, 2015). At the population level, site fidelity is thought to result from intraspecific competition for resources (Bolnick *et al.*, 2003), but populations are often comprised of individuals of varying levels of site fidelity, resulting in the coexistence of behavioural specialists and generalists (Wilson *et al.*, 1994; Arthur *et al.*, 2015; Wakefield *et al.*, 2015; Patrick *et al.*, 2017). However, while there is increasing evidence of the existence of such differences, the individual-level drivers of site fidelity are poorly understood. Individual differences in site fidelity are often attributed to age- or sex-related differences (Phillips *et al.*, 2004; Durell, 2007; Votier *et al.*, 2017), but in many systems, individual variation in site fidelity remains even once age and sex are accounted for (Bolnick *et al.*, 2003; Woo *et al.*, 2008; Votier *et al.*, 2017).

Specialised foraging behaviour may be optimal when resource predictability is high, such that individual differences in site fidelity can emerge as an artefact of spatial partitioning if individuals use foraging areas differing in resource predictability (Switzer, 1993; Barraquand *et al.*, 2008). However, individuals may maintain their level of specialisation over timescales greater than the persistence of resource patches (Wakefield *et al.*, 2015; Patrick *et al.*, 2017), suggesting that individuals can differ intrinsically in degree of specialisation. While foraging differences have been attributed to morphological (van de Pol *et al.*, 2010; Camprasse *et al.*, 2017) and physiological (Bearhop *et al.*, 2004; Watanabe, 2006) variation, significantly less attention has been paid to the influence of individual behavioural variation, or personality differences. Animal personalities are individual differences in behavioural phenotypes, typically measured on behavioural axes, that are consistent over time or context (Gosling, 2001; Réale *et al.*, 2010). The bold–shy personality axis has been linked to various aspects of foraging behaviour, particularly in a spatial context (Patrick *et al.*, 2014; Spiegel *et al.*, 2015). For example, bold and shy individuals have been found to forage over different spatial scales (Patrick *et al.*, 2014; Spiegel *et al.*, 2015) and use different levels of search intensity (van Overveld *et al.*, 2010; Spiegel *et al.*, 2017). Links between boldness and exploration, another commonly studied personality trait which measures space use, are also predicted by the pace-of-life syndrome hypothesis (Réale *et al.*, 2010). Cumulatively, theory and empirical

findings suggest boldness has high potential to promote differences in foraging behaviour, but to our knowledge, no study has examined the relationship between boldness and foraging site fidelity.

As site fidelity has not been incorporated into the personality research framework, there is no unified prediction regarding the relationship between site fidelity and boldness. However, some evidence does suggest that bolder individuals may be more behaviourally specialised. Bold animals generally exhibit inflexible, routine-like behavioural tendencies, while shy individuals show greater flexibility, adapting behaviour to prevailing conditions (Benus *et al.*, 1990; Koolhaas *et al.*, 1999; Wolf *et al.*, 2008; Coppens *et al.*, 2010). Consequently, bold individuals may be more site faithful as they use the same foraging routes and the same foraging sites, whereas shy individuals should show greater variability in use of foraging sites, as they adapt to changing environmental conditions. Alternatively, boldness can lead to spatial partitioning, whereby individuals use mutually exclusive foraging areas (Patrick *et al.*, 2014; Spiegel *et al.*, 2015). If these foraging areas differ in resource predictability, different levels of site fidelity may emerge between bold and shy individuals as an artefact of spatial partitioning. Separating environmental and individual drivers of this relationship is important for elucidating the mechanisms linking personality to specialisation.

In this study, we test whether boldness predicts individual differences in the degree of foraging specialisation in black-legged kittiwakes (*Rissa tridactyla*) breeding at four colonies in Svalbard. Kittiwakes are surface-feeding seabirds which breed in socially monogamous pairs and exhibit biparental care, with both parents incubating eggs and provisioning for chicks until fledging at around 40 days (Coulson, 2011). Kittiwakes are known to show high inter-individual differences in their foraging behaviour and to exhibit varying levels of foraging site fidelity (Irons, 1998; Suryan *et al.*, 2000). We first conducted standardised and repeated novel object tests to assess individuals' positions on the bold–shy continuum. Using GPS loggers we then tracked the foraging movements of kittiwakes over a series of sequential trips to examine individual site fidelity. Specifically, we compared site fidelity in terms of consistent use of foraging locations at sea, and repeatability in the distance, duration and range of foraging trips. We then tested whether boldness leads to spatial partitioning of foraging sites, to examine

whether differences in site fidelity are driven by spatial partitioning. If boldness predicts site fidelity but not spatial partitioning, this would indicate their linkage by individual, rather than environmental mechanisms.

2.0 Methods

2.1 Study system

In 2017, we studied kittiwakes breeding at four colonies on the west coast of Svalbard: Blomstrand (78°59'N 12°07'E), Krykkjefjellet (78°53'N 12°11'E) and Observasjonholmen (78°56'N 12°16'E) in Kongsfjorden, and Grumantbyen (78°10'N 15°05'E) in Isfjorden. Kittiwakes build cup-shaped nests from mud and vegetation (Coulson, 2011). At Grumantbyen, kittiwakes nest on the window ledges of an abandoned building, while at the Kongsfjorden colonies, kittiwakes nest on the ledges of natural cliffs (see Appendix S2.A for more details). Molecular sexing was conducted on DNA extracted from blood and feather samples (Appendix S2.B). All but two individuals were first caught as breeding adults, and birds were therefore of unknown age.

2.2 Boldness tests

We measured individual boldness in response to a novel object, a method routinely used to assess boldness in colonial seabirds (Grace *et al.*, 2014; Patrick *et al.*, 2014) including black-legged kittiwakes (Collins *et al.*, 2019). A full field protocol is provided in Appendix S2.C. An observer presented a novel object (a blue plastic penguin toy, dimensions 13 x 10 x 4.5cm; Munchkin®) to birds on their nests. The object was mounted on the end of an 8m carbon fibre fishing pole, with an action camera (GoXtreme® Wifi) fixed 30cm behind the object recording birds' responses. The observer held the opposite end of the pole from the ground level. Before beginning the test, the observer positioned the novel object at ground level directly beneath the position of the focal nest, where it was out of view of the colony. The observer then raised the object at a constant pace directly upwards towards the nest, until the object rested on the cup of the nest, over a period of 30s. The object was held in position for 60s, before retracting the object and returning it to ground level. Tests were conducted during incubation and early chick rearing. Tests were conducted only when a single adult was attending the nest. Repeat tests were

conducted whenever possible after a minimum of two days, subject to the presence of the focal individual on the nest. A single observer conducted all tests in Isfjorden and a second in Kongsfjorden. Videos were analysed blind by a single observer using JWatcher v1.0 (Blumstein *et al.*, 2007). From the second the object reached the height of the nest, we recorded the proportion of the subsequent 60s the focal bird spent in each of five mutually exclusive behavioural states: (1) sitting on the nest, with the body resting on the nest cup; (2) body raised off nest cup, but not standing; (3) standing on the nest (legs visible and extending to the base of the nest); (4) off the nest but remaining on the cliff or window ledge close to the nest; (5) off the cliff or window ledge (and no longer visible). A total of 133 individuals were tested: 80 were tested once, 29 were tested twice, 15 were tested three times, and 9 were tested more than 3 times (totalling 53 individuals tested more than once).

2.3 GPS tracking

We used GPS loggers to track 50 kittiwakes during incubation and 54 kittiwakes during chick rearing, 19 of which were tracked in both breeding stages. All tracked individuals but one were personality tested (Table S2.A1). Loggers were programmed to record a location every 10-minutes on incubating birds and every 2-minutes on chick-rearing birds (this was to ensure sufficient battery life to record multiple trips per bird during incubation, as incubation trips were known to be substantially longer than chick rearing trips (mean duration 15h vs. 5h; see also Robertson *et al.*, 2014). At one colony (Krykkjefjellet) loggers were also programmed to a 10-minute resolution during chick rearing to meet the data requirements of another study. Birds were equipped with one of three logger types (i-GotU GT120, Mobile Action©; CatLog Gen1 and CatLog Gen2, both http://www.mr-lee.com/sc_supp.htm), a subset of which were refitted with a smaller battery to reduce mass (Table S2.D1). Loggers were sealed in waterproof heat shrink tubing and attached to birds' back feathers using TESA tape, and ranged from 6.3-18.6g in mass (1.5–4.6% of a kittiwake's body mass). We tested whether differences in logger mass influenced foraging behaviour by modelling its effect on the distance, duration and range of foraging trips. We detected no relationship between logger mass and foraging behaviour (Appendix S2.D), and therefore do not discuss these results further in the main results.

Owing to distinctly different foraging behaviour between incubation and chick rearing periods (Robertson *et al.*, 2014; Table 2.1), data were analysed separately by breeding stage. During data processing, we removed points within a 300m buffer of each colony (based on the frequency histogram of point distance to the colony) and defined foraging trips as periods longer than 1h spent outside this buffer (based on the frequency histogram of trip durations; Warwick-Evans *et al.*, 2016). Trips longer than 1h may still include trips carried out for purposes besides foraging, such as bathing. To restrict analyses to foraging trips only, we visually inspected all trips for evidence of detectable foraging behaviour. Seabirds use area-restricted search (ARS) to locate prey, during which movements are characterised by reduced speeds and increased tortuosity (Fauchald *et al.*, 2003). A small number of trips (N = 10: 4 by bold individuals and 6 by shy individuals) contained no evidence of ARS, and were consequently removed from all analyses. All 10 trips were considerably shorter than the mean trip duration (1.5h vs. 10h), which supported that these movements were likely not foraging trips. In total, we recorded 111 foraging trips from 50 individuals during incubation, 31 of which more than one trip was recorded for, and 212 foraging trips from 54 individuals during chick rearing, 45 of which more than one trip was recorded for. All individuals with multiple trips recorded were personality tested (one individual with a single trip recorded during incubation was not personality tested). To standardise data resolution and to account for occasional missing GPS points, we used adehabitatLT (Calenge, 2015) to linearly

Table 2.1. Summary foraging statistics (mean ± SE) and number of trips and individuals tracked for each colony during incubation and chick rearing. Distance metrics are presented in kilometres; time metrics are presented in hours, where 0.5 hours represents 30 minutes.

Colony	Trip metric	Incubation		Chick rearing	
		Metric	N. trips, N. inds	Metric	N. trips, N. inds
Grumantbyen	Distance (km)	552.70 ± 87.12		196.32 ± 23.53	
	Duration (h)	29.52 ± 4.25	32, 16	9.78 ± 1.04	64, 27
	Max. range (km)	186.66 ± 28.92		75.70 ± 8.49	
Blomstrand	Distance (km)	147.44 ± 70.53		47.12 ± 7.76	
	Duration (h)	16.84 ± 3.85	25, 9	4.28 ± 0.41	26, 5
	Max. range (km)	55.70 ± 28.99		15.62 ± 2.32	
Krykkjefjellet	Distance (km)	43.02 ± 9.79		25.10 ± 2.06	
	Duration (h)	11.80 ± 2.88	15, 7	4.48 ± 0.29	37, 8
	Max. range (km)	21.95 ± 9.44		8.73 ± 0.48	
Observasjonholmen	Distance (km)	114.14 ± 37.66		31.99 ± 2.16	
	Duration (h)	38.74 ± 14.78	39, 17	3.72 ± 0.25	85, 13
	Max. range (km)	31.25 ± 9.57		8.43 ± 0.42	

interpolate tracks to intervals of 10-minutes during incubation and 2-minutes during chick rearing.

To identify foraging sites from GPS tracks, we classified each GPS point as one of three behavioural states using hidden Markov models (HMMs). HMMs are a type of state-space model, which decompose observed time series data (here, movement) into a (hidden) sequence of discrete behavioural states. HMMs were fitted using the moveHMM function from the moveHMM package (Michelot *et al.*, 2016), which we provided with starting parameters informed by previous work using HMMs to describe kittiwake foraging behaviour (Trevail et al., 2019; Appendix S2.E). Based on the distributions of step lengths (described by a gamma distribution) and turning angles (described by a von Mises distribution) between consecutive GPS points, HMMs classified each point as one of three behavioural states: foraging, resting, or travelling. We used the Viterbi algorithm to estimate the most likely sequence of states to have generated the observed movement patterns (Zucchini *et al.*, 2016). A three-state model was supported by model selection using AIC, and the three states and their interpretation is consistent with other kittiwake tracking studies (Chivers *et al.*, 2012; Trevail *et al.*, 2019). Consecutive sequences of foraging points were aggregated into foraging sites, and were represented by a single pair of central coordinates (Appendix S2.E). In total, we identified 661 sites during incubation and 1138 sites during chick rearing. Data were separated by breeding stage due to differential temporal data resolution, and by fjord because distributions of step lengths and turning angles differed between the two fjords (Appendix S2.E1), resulting in four HMMs in total.

2.4 Data analysis

We carried out analyses in R v3.5.1 (R Core Team, 2018), using the package *lme4* (Bates *et al.*, 2015) for linear mixed effects models (LMMs). To determine statistical significance of fixed effects, we used ANOVA comparisons of models with and without each variable in turn. We checked model assumptions of normality and homoscedasticity by visual inspection of residual plots.

To estimate individual boldness, we used a Principal Component Analysis (PCA) to collapse the five behaviour variables into a single test score (PC1). We estimated

adjusted repeatability (repeatability after controlling for confounding effects; Nakagawa *et al.*, 2010) of PC1 using the R package *rptR* (Stoffel *et al.*, 2017), including fixed effects to adjust for test date, breeding stage (incubation or chick rearing), observer, and test number. To obtain a single estimate of boldness per individual, we extracted parameter estimates for each individual from a linear model. PC1 was fitted as the response variable, and individual ID, test date, breeding stage, observer, and test number were fitted as fixed effects. We tested for sex differences in boldness estimates in a linear model with sex as a fixed effect.

To quantify foraging site fidelity, we calculated a similarity index following Patrick & Weimerskirch (2017). Briefly, with each site used in turn as the focal site, we randomly paired the focal site with (i) one site used by the same individual on a different foraging trip (within-individual paired site), and (ii) one site from each other individual from the same colony (between-individual paired sites). Site fidelity was estimated only for individuals with more than one trip recorded (N = 31 during incubation; N = 45 during chick rearing), but single-trip birds were retained as between-individual pairs, to compare the focal individual with the full tracked population. The similarity index was then the proportion of between-individual paired sites that were closer to the focal site than the within-individual paired site (Appendix S2.E2). The index is bounded between 0 and 1, and for interpretability this was inverted (1-x) so that values towards 1 indicate high site fidelity (no other individuals foraging more closely to the focal site than the individual's own paired site) and towards 0 indicate low site fidelity (all individuals foraged more closely to the focal site than the individual's own paired site). We ran 1000 iterations of the randomisation, such that each focal site was randomly paired 1000 times. For each model iteration we then fitted a binomial generalized linear model (GLM) with individual ID as a fixed effect to extract a single estimate and standard error of site fidelity for each individual across all of its foraging sites. The time difference (number of days) between paired sites was also included as a fixed effect, to account for variation in temporal proximity between pairs. This resulted in 1000 estimates of site fidelity per individual. Finally, we examined the predictors of site fidelity using a linear model with the following structure: boldness, sex, colony, and date were fitted as fixed effects, and the two-way interactions between boldness and sex, and boldness and colony were included. Site fidelity was fitted as the response variable, and as the randomisation

generated 1000 estimates of site fidelity per individual (one from each iteration of the randomisation), the model was ran 1000 times also, using a loop to set the site fidelity estimates produced by each iteration of the randomisation (Patrick *et al.*, 2015). We present 95% confidence intervals for model estimation based on the 1000 model iterations (Nicolaus *et al.*, 2012).

To test for spatial partitioning by boldness, we examined whether variation in boldness was associated with geographic variation in foraging sites. To do this, we modelled the central latitude (log2 transformed to approach normality) and longitude (square-root transformed to approach normality) of foraging sites using LMMs. Trip ID nested within bird ID was fitted as a random effect to adjust for multiple foraging sites within a trip, and multiple trips per individual. Boldness, sex, colony, and date were fitted as fixed effects, and the two-way interactions between boldness and sex, and boldness and colony were included. We additionally tested for a relationship between boldness and the extent to which a bird's foraging distribution overlapped with the colony-level distribution, and found no evidence for a relationship (see Appendix S2.F).

Wide-ranging animals such as seabirds can be specialised in aspects of space use besides spatial locations of foraging behaviour. To quantify other measures of foraging specialisation, we examined three summary metrics of foraging trips: (1) mean foraging trip distance (km); (2) mean foraging trip duration (hours); (3) mean maximum range from the colony (km). Occasionally recordings of foraging trips were incomplete due to logger failure (N = 39). These trips were excluded from our calculations of trip distance and duration, and were only included in calculation of maximum range from the colony if the bird had returned within 75% of the maximum distance from the colony before logger failure (N = 18; Paredes et al., 2012). To test whether boldness was associated with specialisation in each foraging trip metric, we grouped individuals by boldness scores and compared repeatability of trip metrics between groups, since repeatability is a group-level measure of individual consistency (Nakagawa *et al.*, 2010). Based on the median boldness score, birds were categorised as either "bold" (higher values) or "shy" (lower values), resulting in 67 bold individuals and 66 shy individuals. We estimated repeatability of trip distance, duration, and maximum range (all log10 transformed) for bold and shy birds separately, and checked for non-overlapping 84% confidence

intervals between bold and shy birds, since the absence of overlap between 84% confidence intervals is equivalent to a z-test at the 0.05 level (Aplin et al., 2015; Payton, Greenstone, & Schenker, 2003; Tryon, 2001).

To avoid issues pertaining from multicollinearity we were unable to include both date and chick age as fixed effects in models on chick rearing data. While birds may adjust foraging behaviour with chick age (Christensen-Dalsgaard *et al.*, 2018), bold and shy kittiwakes did not differ in the age of their chicks at logger deployment (Appendix S2.D), and therefore any detected effects of boldness are unlikely to be mediated by differences in chick age at tracking.

3.0 Results

3.1 Boldness

PC1 explained 61% of the variance in the response to the novel object (see Table 2.2 for variable loadings). Boldness scores ranged from -1.690 to 1.519 with low values representing instances when birds left the nest, medium values representing instances when birds remained on the nest but stood or raised up, and high values representing instances when birds did not adjust stance. Low values of PC1 were interpreted as "shy" responses, and high values as "bold" responses. Kittiwakes were highly repeatable in response to the novel object ($R = 0.678$, CI: 0.572-0.791; $p < 0.001$). We detected no difference in boldness between the sexes ($F_{1,129} = 2.863$; $p = 0.098$).

Table 2.2. Principal Component Analysis output for boldness scores.

Behaviour	PC1	PC2	PC3	PC4	PC5
Sitting	0.743	0.462	-0.118	0.144	0.447
Raised up	-0.001	-0.639	-0.600	0.178	0.447
Standing	-0.043	-0.291	0.754	0.381	0.447
Off the nest	-0.032	-0.069	0.151	-0.878	0.447
Off the ledge	-0.667	0.537	-0.186	0.175	0.447
Cumulative variance explained	0.612	0.845	0.948	1.000	1.000

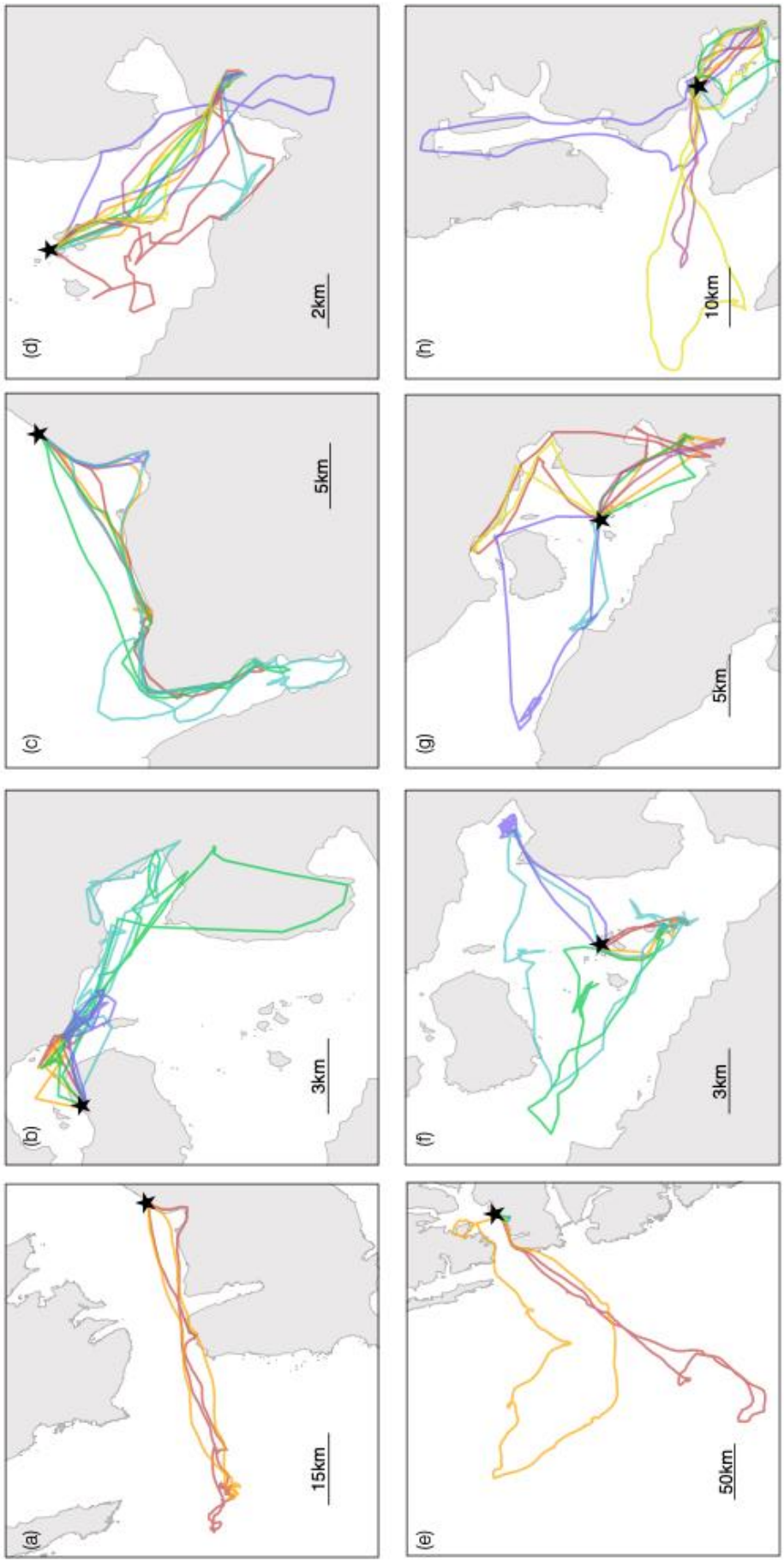

Figure 2.1. Differences in foraging site fidelity between bold and shy kittiwakes. Top row shows repeated foraging trips from four different bold individuals (a: *N* = 2 trips; b: *N* = 5 trips; c: *N* = 5 trips; d: *N* = 7 trips). Bottom row shows repeated foraging trips from four different shy individuals (e: *N* = 3 trips; f: *N* = 5 trips; g: *N* = 7 trips; h: *N* = 7 trips). Trips are colour-coded chronologically: 1 = red; 2 = orange; 3 = green; 4 = blue; 5 = purple; 6 = pink; 7 = yellow. Colony locations are marked by black stars.

Table 2.3. Results for the effects of boldness, sex, date, and colony on site fidelity and spatial partitioning (latitudinal and longitudinal locations of foraging sites). Significant terms are indicated in bold. Two-way interactions between boldness and sex, and boldness and colony, were found to be non-significant and dropped from all models (results presented in the text). Estimates for sex effects are presented as the difference for males over females. Estimate range for site fidelity models are the 95% confidence intervals extracted from a model that uses 1000 estimates of site fidelity per individual, included to incorporate individual variability in site fidelity.

	Response	Model output	Boldness	Sex (male)	Date	Colony
Incubation	Site fidelity	Estimate ± SE	0.086 ± 0.024	0.059 ± 0.064	0.036 ± 0.081	
		Test statistic	$F_{1,25}$ = 13.391	$F_{1,25}$ = 1.333	$F_{1,25}$ = 1.812	$F_{3,27}$ = 2.493
		P value	**p = 0.003**	p = 0.359	p = 0.264	p = 0.130
		Estimate range	0.085 – 0.087	0.053 – 0.064	0.027 – 0.045	
	Site latitude	Estimate ± SE	-0.059 ± 0.036	-0.048 ± 0.076	0.039 ± 0.038	
		Test statistic	χ^2_1 = 2.855	χ^2_1 = 0.382	χ^2_1 = 0.890	χ^2_3 = 109.310
		P value	p = 0.097	p = 0.537	p = 0.346	**p < 0.001**
	Site longitude	Estimate ± SE	-0.028 ± 0.041	-0.177 ± 0.086	-0.022 ± 0.044	
		Test statistic	χ^2_1 = 0.477	χ^2_1 = 4.398	χ^2_1 = 0.307	χ^2_3 = 5.694
		P value	p = 0.490	**p = 0.036**	p = 0.580	p = 0.128
Chick rearing	Site fidelity	Estimate ± SE	0.005 ± 0.040	0.098 ± 0.076	-0.027 ± 0.185	
		Test statistic	$F_{1,36}$ = 0.097	$F_{1,36}$ = 1.768	$F_{1,36}$ = 0.110	$F_{3,38}$ = 0.782
		P value	p = 0.811	p = 0.232	p = 0.794	p = 0.544
		Estimate range	0.004 – 0.005	0.093 - 0.102	-0.038 - -0.015	
	Site latitude	Estimate ± SE	0.009 ± 0.006	-0.030 ± 0.012	0.009 ± 0.008	
		Test statistic	χ^2_1 = 2.531	χ^2_1 = 6.075	χ^2_1 = 1.216	χ^2_3 = 456.020
		P value	p = 0.112	**p = 0.014**	p = 0.270	**p < 0.001**
	Site longitude	Estimate ± SE	0.008 ± 0.017	-0.015 ± 0.035	0.047 ± 0.024	
		Test statistic	χ^2_1 = 0.210	χ^2_1 = 0.175	χ^2_1 = 3.058	χ^2_3 = 45.548
		P value	p = 0.647	p = 0.676	p = 0.054	**p < 0.001**

3.2 Site fidelity

Site fidelity was variable between birds during both breeding stages (incubation: median = 0.588, range = 0.291 – 0.846; chick rearing: median = 0.554, range = 0.332 – 0.933; Figure 2.1-2.2). Boldness was positively related to site fidelity during incubation ($F_{1,25}$ = 13.391, p = 0.003; Figure 2.2; Table 2.3), with bolder individuals showing higher faithfulness to foraging sites than shy individuals. No relationship between boldness and site fidelity was found during chick rearing (Figure 2.2; Table 2.3). There was no interaction between boldness and sex (incubation: $F_{1,21}$ = 0.287, p = 0.689; chick rearing: $F_{1,32}$ = 0.178, p = 0.739) or between boldness and colony (incubation: $F_{3,23}$ = 0.912, p = 0.512; chick rearing: $F_{3,34}$ = 0.692, p = 0.585) on site fidelity.

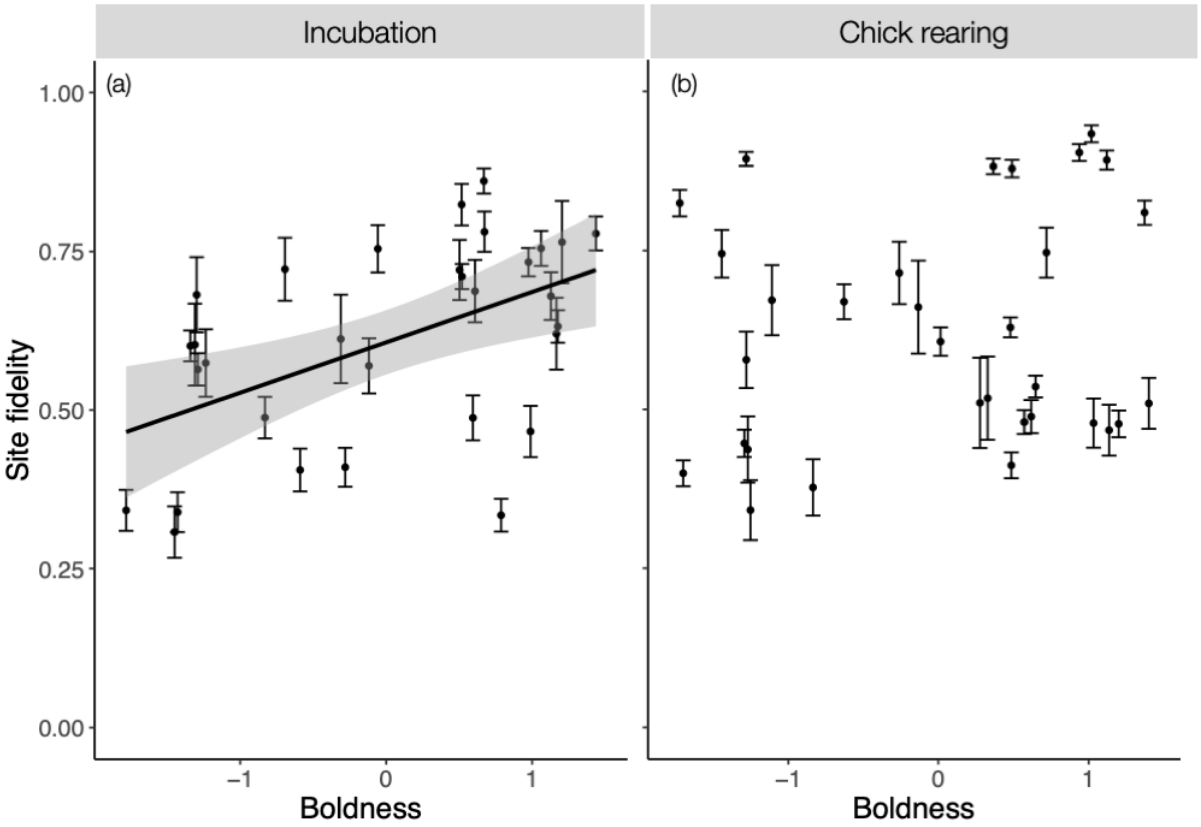

Figure 2.2. The relationship between boldness and foraging site fidelity. Data were separated by breeding stage into incubation foraging trips (a) and chick rearing foraging trips (b). High values indicate highly site faithful individuals. We present mean values of site fidelity (± S.E.) for each individual. Bolder individuals showed lower estimates of foraging site fidelity during incubation (a) but not during chick rearing (b).

3.3 Foraging trip repeatability

Foraging trips were longer in duration and further in distance and range during incubation compared to during chick rearing (Table 2.1). During incubation, bold kittiwakes were more repeatable than shy birds in foraging trip duration (bold: R = 0.162, CI = 0.113, 0.208; shy: R = 0.051, CI = 0.032, 0.085) and range (bold: R = 0.185, CI = 0.129, 0.243; shy: R = 0.001, CI = 0.000, 0.001; Figure 2.3a), while foraging trip distance was not repeatable regardless of personality (R = 0.072). During chick rearing bold kittiwakes were more repeatable in foraging trip distance (bold: R = 0.543, CI = 0.466, 0.624; shy: R = 0.000, CI = 0.000, 0.000), duration (bold: R = 0.502, CI = 0.401, 0.587; shy: R = 0.130, CI = 0.098, 0.184), and maximum range (bold: R = 0.494, CI = 0.403, 0.575; shy: R = 0.029, CI = 0.011, 0.038; Figure 2.3b).

3.4 Boldness and spatial partitioning of foraging distributions

We found no evidence for spatial partitioning by boldness in kittiwakes, as boldness did not predict the latitude and longitude of foraging sites during either breeding stage. We found no evidence for interacting effects of boldness with sex on spatial partitioning (incubation: boldness × sex on latitude: $\chi^2_1 = 0.121$, $p = 0.729$; boldness × sex on longitude: $\chi^2_1 = 1.276$, $p = 0.259$. Chick rearing: boldness × sex on latitude: $F_{1,46} = 0.257$, $p = 0.614$; boldness × sex on longitude: $\chi^2_1 = 3.156$, $p = 0.076$), or boldness and colony (incubation: boldness × colony on latitude: $\chi^2_3 = 6.127$, $p = 0.106$; boldness × colony on longitude: $\chi^2_3 = 2.214$, $p = 0.529$. Chick rearing: boldness × colony on latitude: $\chi^2_3 = 3.707$, $p = 0.295$; boldness × colony on longitude: $\chi^2_3 = 0.530$, $p = 0.912$). Females utilised sites further east than males during incubation (Table 2.3).

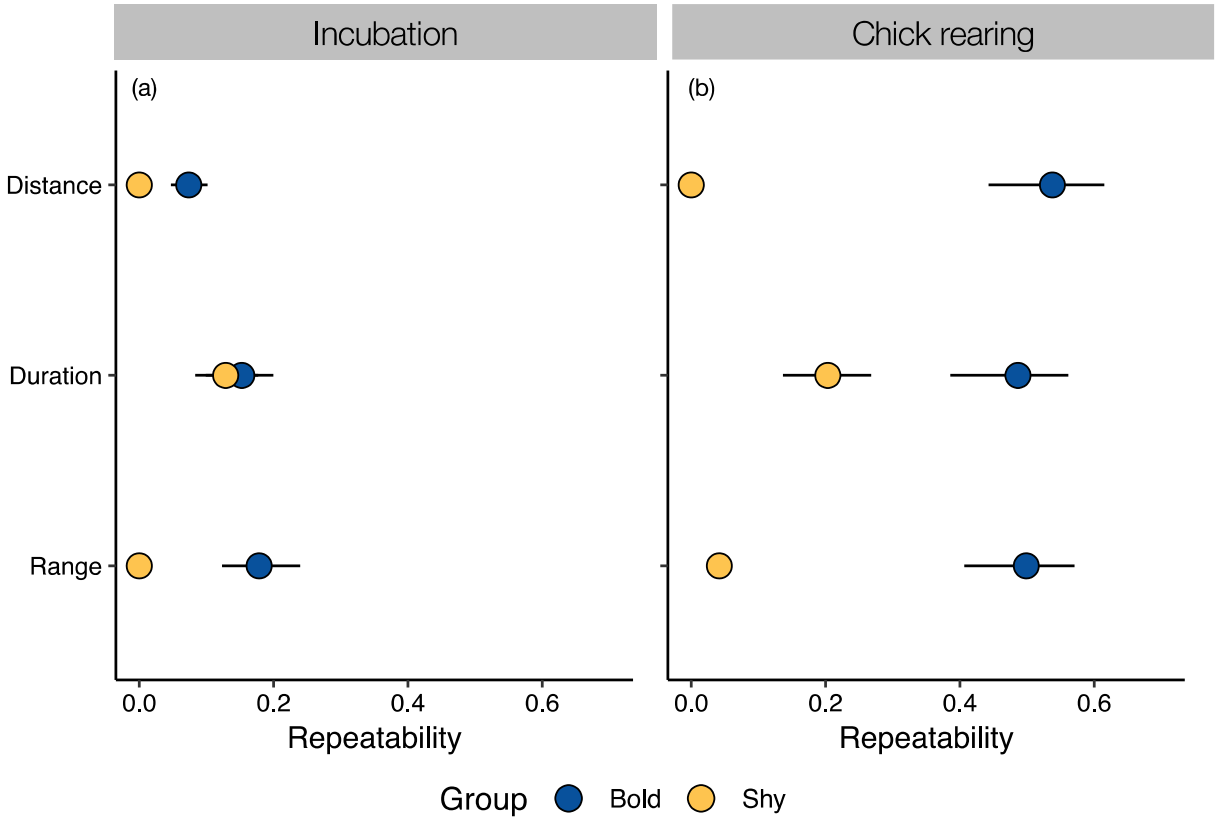

Figure 2.3. Repeatability of the distance, duration and maximum range of foraging trips made by shy and bold birds. Results are shown during incubation trips (a) and chick rearing trips (b). Dark blue points indicate bold individuals, yellow points indicate shy individuals. While boldness is otherwise a continuous measure, here individuals were grouped by boldness to be able to compare differences in repeatability (since repeatability is a group-level measure). 84% confidence intervals are displayed: non-overlapping 84% confidence intervals are equivalent to z-tests at the 0.05 level.

4.0 Discussion

Individual differences in foraging specialisation were linked to boldness in black-legged kittiwakes across multiple colonies. Individual kittiwakes varied in their level of foraging site fidelity, and in line with our predictions, bolder kittiwakes exhibited higher foraging site fidelity than shy individuals, providing the first demonstration that personality is related to site fidelity. This relationship was present during incubation but not chick rearing. In addition, during both incubation and chick rearing, bolder birds were more repeatable in their foraging trips than shy individuals, indicating that bold individuals were more specialised, and shy individuals more generalised, in their behaviour. We found no evidence of boldness-dependent spatial partitioning: boldness was not associated with foraging at particular latitudes or longitudes, indicating that bold and shy individuals exhibited different levels of specialisation while foraging over the same areas. Together, these results suggest that personality differences may constitute important predictors of differences in individual foraging specialisations.

4.1 Differences between breeding stages

In keeping with previous work on kittiwakes (Irons, 1998), we observed individual differences in foraging site fidelity, demonstrating the coexistence of specialist and generalist foraging strategies. Median site fidelity did not differ between incubation and chick rearing, but we found that birds were markedly more repeatable in the distance, duration and range of their foraging trips during chick rearing compared to during incubation. Shifts in foraging strategies between incubation and chick rearing periods have previously been reported in kittiwakes (Robertson *et al.*, 2014), and may result from seasonal changes in resource availability, for example due to the depletion of prey patches (Birt *et al.*, 1987). However, we found no evidence of a linear change in site fidelity with date, which would indicate behavioural changes to match shifting resource distributions. Instead, we suggest that increased consistency during chick rearing is likely linked to concomitant reductions in trip length, due to the increased demands of the chick rearing period (Weimerskirch *et al.*, 1993). During incubation in many seabird species, birds make longer trips to profitable foraging grounds that are presumably out of reach after hatching, when time spent away from the nest is constrained by offspring demand for provisioning (Phillips *et al.*, 2004; Robertson *et al.*, 2014). Despite foraging trips being less consistent in length during incubation, average levels of site fidelity were

similar in incubation to during chick rearing, demonstrating that returning to previous foraging locations is a favoured strategy even when adults are less constrained in their foraging movements.

4.2 Site fidelity without spatial partitioning

Previous studies have linked boldness to spatial aspects of foraging, including home range size (Boon *et al.*, 2008), and search methods (Wesley *et al.*, 2012), but evidence linking personality to foraging site fidelity has been lacking. Our finding that bold individuals were more site faithful than shy individuals during incubation was coupled with a lack of spatial partitioning. The significance of a lack of spatial partitioning is that the relationship between boldness and site fidelity appears not to be driven by differences in habitat availability, at least at the broad spatial scale: instead, it suggests a behavioural difference between individuals occupying the same environment. Behavioural differences in foraging movements between bold and shy individuals are also evident in the fact that bold individuals were more repeatable in foraging trip metrics, during both incubation and chick rearing. Below, we outline potential causes of our findings.

4.3 Boldness and foraging site fidelity

Shy birds were less site faithful than bold birds, but only during incubation, potentially owing to constraints on behavioural flexibility during the chick rearing period. As bold and shy individuals appear to share habitat availability, their differences in site fidelity during incubation suggest different responses to the environment. In predictable environments, returning to previous foraging locations should be favoured; conversely, in unpredictable habitats the probability of a previous location being profitable again is low, and consequently animals should show lower site fidelity and greater reliance on environmental cues to locate prey (Switzer, 1993; Weimerskirch *et al.*, 2005). The marine environment is characterised by both persistent oceanographic features (bathymetric structures, fronts) which generate predictable prey patches, as well as highly dynamic tidal and weather processes which result in spatiotemporally variable resource distributions (Scales *et al.*, 2014; Cox *et al.*, 2016). High and low reliance on environmental cues may represent alternative foraging tactics that can both be profitable within the same macro-scale habitat (Carroll *et al.*, 2018). Our findings suggest

that shy and bold kittiwakes may differ in their propensity to adopt these two tactics, with bold individuals showing lower sensitivity to environmental cues than shy individuals, but that during the chick rearing period, shy individuals switch to a high site fidelity foraging strategy.

Shyer animals are often characterised by high responsiveness to change (Wolf *et al.*, 2008; Coppens *et al.*, 2010), and indeed, in our boldness test, shy individuals were more responsive to the presentation of a novel object. Previous work has linked boldness with responsiveness to environmental change: for instance, shy, but not bold, Atlantic cod (*Gadus morhua*) adjust their home ranges in response to increases in sea temperature (Villegas-Ríos *et al.*, 2018), and in sleepy lizards (*Tiliqua rugosa*) shy individuals were more responsive to changes in resource availability (Spiegel *et al.*, 2015). During incubation, when birds are less constrained to return to predictable foraging sites, shy individuals may therefore be more likely to select sites based on environmental cues, rather than based on previous foraging attempts. Reliance upon environmental cues may extend to social indicators of foraging opportunities, with some studies suggesting that shy individuals rely more heavily on social information when making foraging decisions (Kurvers *et al.*, 2010; Aplin *et al.*, 2014)

Bolder, competitive individuals may make more use of reliable foraging patches (e.g. van Overveld et al., 2018). A study on black-browed albatross (*Thalassarche melanophrys*) found that bold birds foraged in areas associated with high competition, while shy individuals avoided these regions (Patrick *et al.*, 2014). Due to their increased propensity to engage in competitive interactions (Sih *et al.*, 2004; Dammhahn *et al.*, 2012), bold individuals may consistently use predictable foraging hotspots, while shy individuals avoid such areas when able to do so, and instead forage more variably in less predictable habitat. In Arctic waters, glacial zones constitute key foraging habitat for kittiwakes, and represent highly predictable and detectable foraging areas (Lydersen *et al.*, 2014). Accordingly, glaciers may represent such foraging hotspots that could be disproportionately used by bold and not shy kittiwakes in Svalbard. The next step to test for personality-dependent habitat selection requires models of oceanographic conditions across the population's foraging range, to examine whether shy and bold

kittiwakes select foraging areas associated with different levels of predictability and competition.

While shy animals typically exhibit flexibility in response to environmental fluctuations, bolder animals are instead thought to rely upon routines when navigating (Benus *et al.*, 1990; Marchetti *et al.*, 2000; Coppens *et al.*, 2010). For example, bold great tits (*Parus major*) were found to quickly develop a routine-like search pattern of feeding sites, and were robust in following routines even when sites have been unprofitable on previous visits, while shy birds were more likely to visit new sites (Verbeek *et al.*, 1994). When locating foraging sites, bold kittiwakes may navigate by routine-like behavioural tendencies, resulting in higher return rate previously visited sites. Our results comparing repeatability of foraging trips lend further support to this suggestion: bold kittiwakes made foraging trips that were more consistent in distance, duration and range than shy individuals, which may reflect routine-like usage of the same routes to foraging sites in bolder birds. Interestingly, during chick rearing, bold birds continued to make foraging trips that were markedly more consistent in length than the trips of shy individuals, while bold and shy birds showed no differences in site fidelity. This suggests even when constrained by offspring provisioning to return to known, reliable sites, bold and shy birds differ in how they navigate to these locations.

5.0 Conclusions

Our study found that a widely studied personality trait, boldness, predicts more specialised and consistent foraging behaviour during the breeding season in four colonies of kittiwakes. Studies of specialised foraging behaviour often overlook variation in individuals' level of specialisation (but see Grecian *et al.*, 2018; Patrick & Weimerskirch, 2017; Votier et al., 2017; Wakefield et al., 2015). While site fidelity may have consequences for individual fitness (Authier *et al.*, 2012; Patrick *et al.*, 2017), coexistence of specialists and generalists suggests that site fidelity may be under fluctuating selection (Wilson *et al.*, 1994; van de Pol *et al.*, 2010) or frequency dependent selection (Fitzpatrick *et al.*, 2007). Here, we suggest that individual differences in site fidelity may also be maintained through association with personality traits. In another

seabird species, boldness has been shown to be a heritable trait and repeatable between years (Patrick *et al.*, 2013), and therefore has the potential to result in differences in foraging behaviour under selection. Despite an increased move towards individual-based approaches in foraging and movement ecology, individual drivers of variation in behaviours such as site fidelity are commonly overlooked, and the number of studies considering factors beyond age and sex are even rarer. Future studies on individual foraging specialisations should also consider examining the combined effects of personality differences with other factors, such as age, or variability in environmental factors such as prey distributions. We advocate the importance of considering phenotypic-level behavioural traits such as boldness to improve understanding of variation in behavioural specialisation.

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Author contributions

S.M.H., S.C.P., S.D., and L.U.S. conceived the study and the methodology. S.M.H. conducted statistical analysis and wrote the manuscript. S.M.H, S.C.P., S.D., P.B. and O.C. conducted the fieldwork. All authors contributed substantially to production of the manuscript.

Data accessibility

Data are accessible from the Dryad Digital Repository:

https://datadryad.org/resource/doi:10.5061/dryad.221f9g2

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Supplementary Materials to Chapter 2: Personality predicts foraging site fidelity and trip repeatability in a marine predator

Appendix S2.A – Colony details

Table S2.A1. Details of black-legged kittiwake colonies studied in 2017. Colony size is the estimated number of breeding pairs in 2017. Number of kittiwakes tested for boldness, tracked during incubation, and tracked during chick rearing are presented by colony, along with total across all colonies, and total across all colonies that were tested more than once/tracked for more than one trip at the bottom. Numbers in parentheses indicate number of tracked individuals that were also tested for boldness. Not all personality tested individuals were tracked, and not all tracked individuals were personality tested, but all personality tested individuals (including those not tracked) were included in the estimation of boldness and its repeatability; all tracked individuals (including those not boldness tested) were included the estimation of individual foraging site fidelity.

Fjord Colony	Coordinates	Colony size	N. boldness tested	N. tracked: incubation	N. tracked: chick rearing
Isfjorden					
Grumantbyen	78°10'N 15°05'E	50	62	16 (16)	27 (27)
Kongsfjorden					
Blomstrand	78°59'N 12°07'E	900	25	9 (9)	5 (5)
Krykkjefjellet	78°53'N 12°11'E	200	19	8 (7)	9 (8)
Observasjonholmen	78°56'N 12°16'E	150	27	17 (17)	13 (13)
Total			133	50 (49)	54 (54)
Total w/ repeat measures			53	31 (31)	45 (45)

Appendix S2.B – Molecular sexing methodology

Sex was determined after DNA extraction by polymerase chain reaction (PCR). Genomic DNA was extracted from blood and feathers using DNeasy 96 Blood and Tissue Kit (Qiagen, Hilden, Germany) following the manufacturer's protocol. Sex was determined using the primers M5 (Bantock *et al.*, 2008) and P8 (Griffiths *et al.*, 1998). These primers amplify the sex-linked CHD-W and CHD-Z genes, which differ in length and result in a single band for males and two bands for females. The M5 primer was 6FAM fluoro-labelled. Polymerase chain reaction (PCR) was performed with Qiagen's Multiplex PCR Kit following the manufacturer's protocol, but using 8.4 µL reaction volume. PCR products were mixed with GeneScan 500 LIZ (Applied Biosystems) size standard and Hi-Di formamide. Alleles were separated using capillary electrophoresis on an ABI 3500xl Genetic Analyzer and sizes assigned using GeneMapper software (Applied Biosystems).

Appendix S2.C – Boldness test protocol

Protocol for measurement of boldness in the field:

- Fully extend the pole before beginning the test. Ensure no other person is in front of the colony before beginning.
- When ready to test a bird, start the video recording and note down the exact time on the camera.
- Position yourself in front of the position of the focal bird's nest, with the object at ground level beneath the nest.
- During the test, minimise all movements besides raising the pole, refrain from speaking, and avoid staring directly at birds.
- Slowly and steadily, over approx. 30s, raise the pole towards the focal bird on the nest, taking care to avoid sudden movements with the object or contact with the cliff/building. Aim to keep the pole at a 90° angle to the building as you raise it. Raise the pole by sliding it through the hands, wearing gloves if necessary to make the motion smooth.
- Bring the object to rest on top of the cup of the nest. Immediately begin timing and hold the object in place here for 60s.
- If the bird leaves the nest during the test, keep the object in place for the full 60s to record whether the bird returns.
- After 60s, carefully bring the object directly down to the ground, and stop the video recording. Move away from the colony before speaking.
- If two members of the pair are at the nest (i.e. during a changeover event), do not test either bird, but instead return later to test when only one bird is present.

Example videos of test responses can be found at:

https://drive.google.com/drive/folders/13dTn4RaMo0F776PE4tQZ71soAR9RrwPN?usp=sharing

Appendix S2.D – GPS tracking

S2.D1 GPS logger models and masses

Kittiwakes were equipped with one of three different GPS logger models (i-GotU GT-120; CatLog Gen1, CatLog Gen2). To reduce logger mass, we modified a number of i-GotU and CatLog Gen1 loggers to carry a smaller battery (2.22 – 4.47g lighter). Sample sizes for each type of logger are provided in Table S2.D1 (number deployed).

Table S2.D1: Sample sizes of different GPS logger models and battery combinations.

GPS logger model	Battery	Average mass (g) ± SD	Number used
i-GotU GT-120	Original	17.75 ± 0.59	23
i-GotU GT-120	Modified	13.28 ± 0.63	102
CatLog Gen1	Original	15.10 ± 0.34	6
CatLog Gen1	Modified	12.88 ± 0.43	10
CatLog Gen2	Original	7.18 ± 0.44	33

S2.D2 Effects of logger mass on foraging behaviour

We tested whether differences in logger mass influenced foraging behaviour (foraging trip distance, duration, and maximum range from the colony), using linear models with the same model structure used in models of site fidelity and site selection. Distance, duration and range were all log10 transformed. Models were split by breeding stage. We found no effect of GPS logger mass on the distance (incubation: $F_{(1,37)} = 0.84$, $p = 0.77$; chick rearing: $F_{(1,43)} = 0.13$, $p = 0.72$), duration (incubation: $F_{(1,37)} = 1.90$, $p = 0.17$; chick rearing: $F_{(1,43)} = 0.12$, $p = 0.73$), and range of trips (incubation: $F_{(1,45)} = 0.94$, $p = 0.34$; chick rearing: $F_{(1,43)} = 0.01$, $p = 0.91$). This indicates that variation in logger mass within the range used in our study was unlikely to drive differences in foraging behaviour.

S2.D3 Variation in chick age at logger deployment

The age of chicks at logger deployment (during the chick rearing phase) was variable (2-21 days), but we were unable to test of an effect of chick age due to strong collinearity with date. However, chick age at logger deployment did not correlate with boldness ($F_{(1,46)} = 0.19$, $p = 0.66$), hence effects of differences in chick age are unlikely to have biased our conclusions.

Appendix S2.E – Hidden Markov models and foraging site fidelity

S2.E1 Hidden Markov models

Owing to different resolutions of tracking data during incubation and chick rearing stages (10 min and 2 min intervals, respectively), we separated hidden Markov models (HMMs) by breeding stage. We additionally separated data by fjord (Isfjorden and Kongsfjorden), because kittiwake movement differed substantially in the distribution of step lengths and turning angles between the two fjords (see histograms in Figure S2.E1 for incubation data and S2.E2 for chick rearing data), and combined models resulted in poor classification of data. As a result, we ran four HMMs, the starting parameters for which are detailed in Table S2.E1. Figures S2.E1 and S2.E2 show the HMM fitted behavioural state distributions classified overlaying the histograms of observed step length and turning angle distributions.

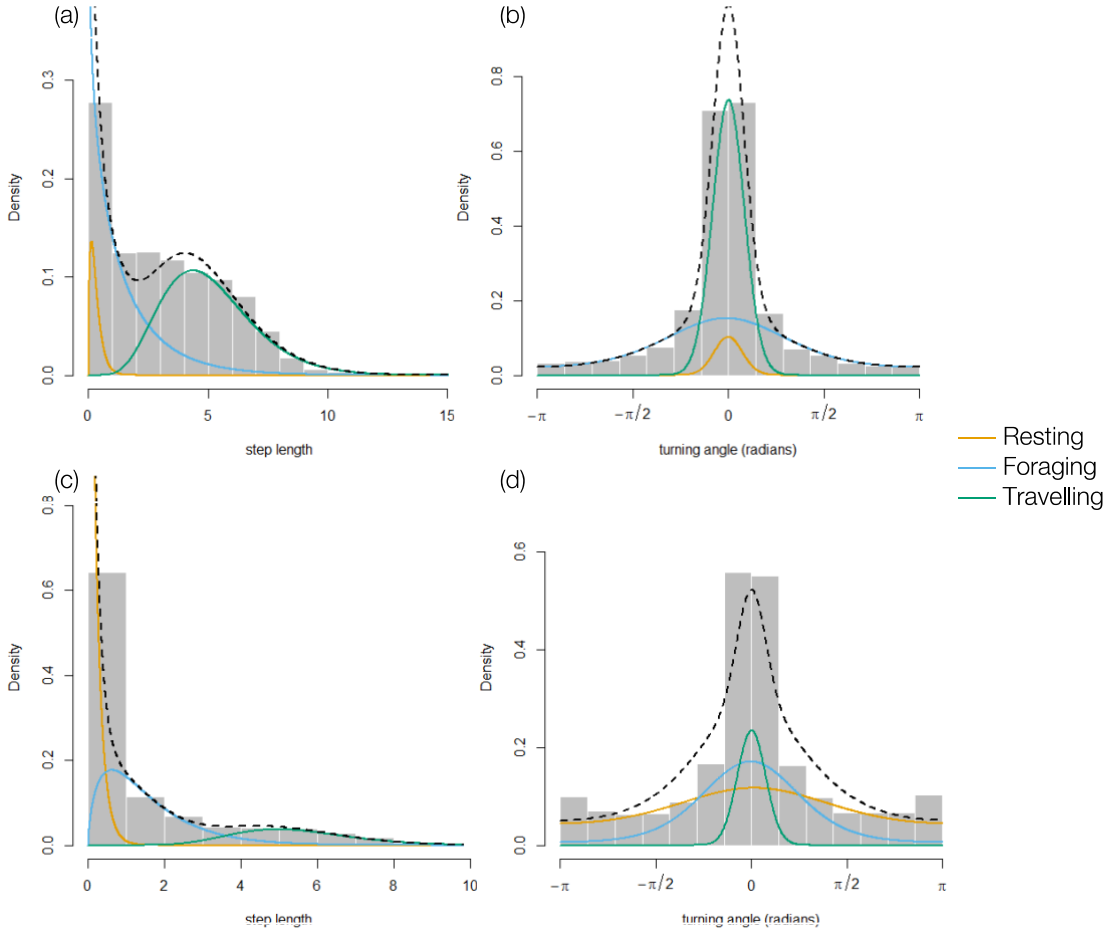

Figure S2.E1: Histograms of (a, c) observed step lengths and (b, d) observed turning angles between consecutive GPS points during incubation for kittiwakes in Isfjorden (a, b) and Kongsfjorden (c, d). Coloured lines indicate HMM fitted state distributions (yellow: resting; blue: foraging; green: travelling).

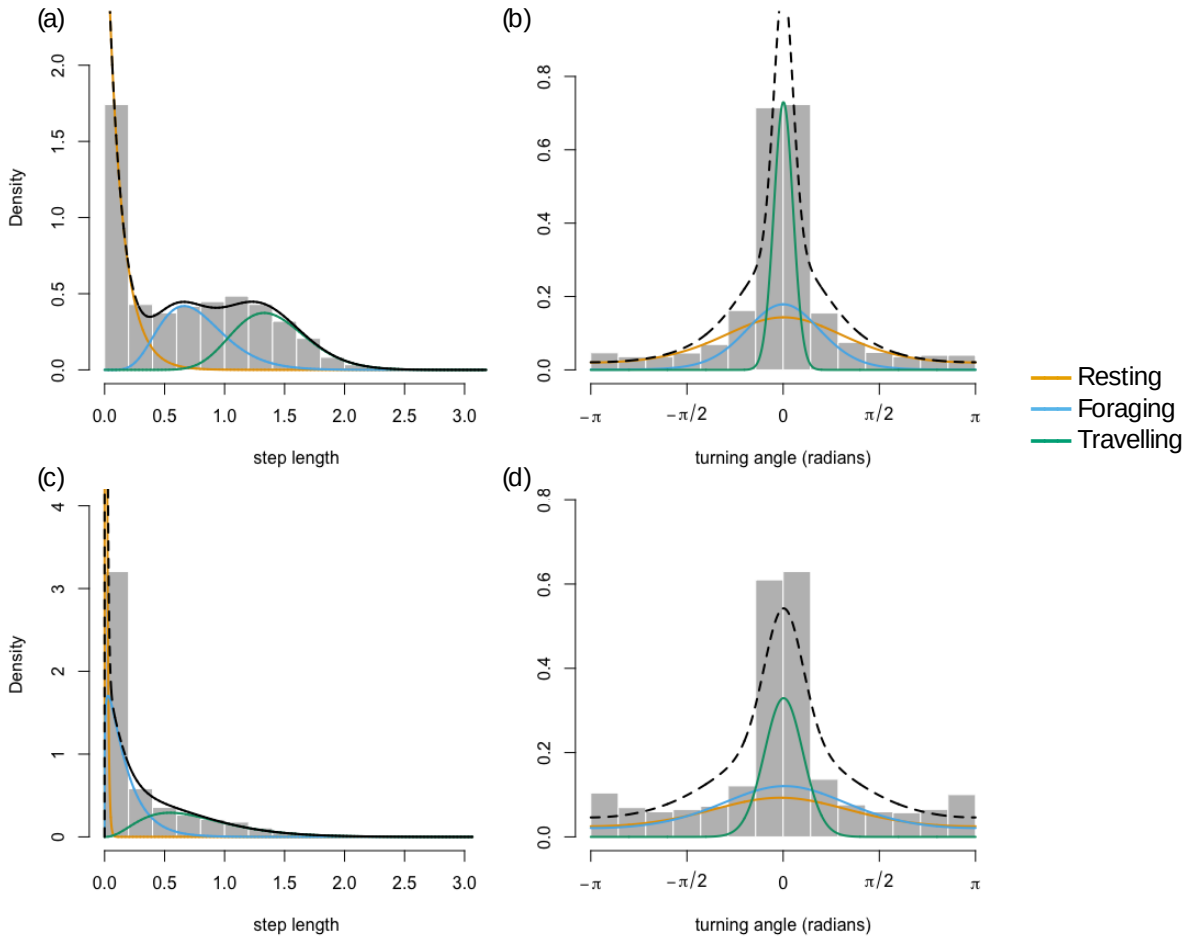

Figure S2.E2: Histograms of (a, c) observed step lengths and (b, d) observed turning angles between consecutive GPS points during chick rearing for kittiwakes in Isfjorden (a, b) and Kongsfjorden (c, d). Coloured lines indicate HMM fitted state distributions (yellow: resting; blue: foraging; green: travelling).

Table S2.E1. Starting parameters (SL: step length; TA: turning angle) for each HMM.

	Incubation		Chick rearing	
Behaviour	Isfjorden	Kongsfjorden	Isfjorden	Kongsfjorden
Resting	SL: 0.10 ± 0.20 TA: μ = 0, κ = 14	SL: 0.20 ± 0.20 TA: μ = 0, κ = 0.5	SL: 0.02 ± 0.04 TA: μ = pi, κ = 0.5	SL: 0.02 ± 0.04 TA: μ = pi, κ = 0.5
Foraging	SL: 2.00 ± 1.50 TA: μ = 0, κ = 0.4	SL: 2.00 ± 2.00 TA: μ = pi, κ = 3.0	SL: 0.15 ± 0.2 TA: μ = 0, κ = 0.5	SL: 0.15 ± 0.2 TA: μ = 0, κ = 0.5
Commuting	SL: 5.00 ± 2.00 TA: μ = 0, κ = 7	SL: 5.00 ± 5.00 TA: μ = 0, κ = 0.5	SL: 1.2 ± 0.5 TA: μ = 0, κ = 3	SL: 1.2 ± 0.5 TA: μ = 0, κ = 3

S2.E2 Similarity index to estimate individual foraging site fidelity

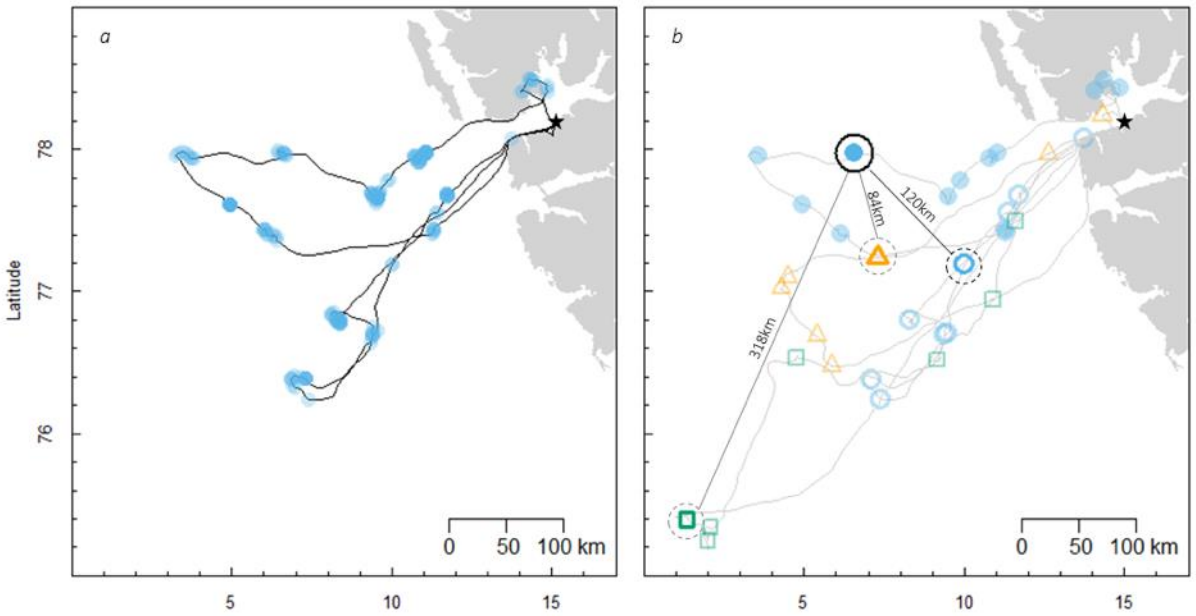

Figure S2.E3. Methods used to estimate individual foraging site fidelity. a) First, GPS points on foraging trips (here two trips by the same individual are shown) were classified as either resting, travelling, or foraging behaviour (coloured in blue) using hidden Markov models. b) Consecutive sequences of points classified as foraging were deemed foraging sites, represented by the central coordinates of those sites. Here, sites used by three birds are indicated by symbols (individual ID represented by symbol; open and filled symbols represent two different trips made by the same individual). For each site in turn as the focal site (here circled in black), focal sites were randomly paired with i) a within-individual site (a site used by the same individual on a different trip), and ii) a number of between individual sites (one site used by each other tracked individual). Here three paired sites are circled with a dashed line. The similarity index calculates the proportion of between-individual sites closer to the focal site than the within-individual site, here = 1/2 and so similarity = 0.5.

Appendix S2.F – Testing for an effect of boldness on foraging distribution overlap

In addition to testing whether boldness was associated with linear geographic spatial partitioning, we used kernel density estimation (KDE) to test for a relationship between boldness and the extent to which birds' foraging distributions overlap with that of the colony. We calculated 95% KDEs for each individual and the joint 95% KDE for all individuals within the same colony, with a grid size of approximately $5km^2$ and using the *href* algorithm to optimise the smoothing parameter (Calenge, 2006). Each individual's overlap with the colony-level KDE was then estimated using the kerneloverlapHR function (Calenge, 2006), where 0 indicates no overlap and 1 indicates complete overlap with the colony -level foraging distribution. We tested whether KDE overlap was related to boldness by fitting it as the response variable in a linear model with boldness, sex, colony, and date were fitted as fixed effects, and the two-way interactions between boldness and sex, and boldness and colony included.

We found no evidence that boldness predicts individuals' KDE overlap with the colony-level KDE (Table S2.F1), nor an interaction between boldness and sex (incubation: $F_{1,42} = 0.890$, $p = 0.351$; chick rearing: $F_{1,46} = 1.449$, $p = 0.235$) or boldness and date (incubation: $F_{3,41} = 0.471$, $p = 0.705$; chick rearing: $F_{3,45} = 0.331$, $p = 0.803$) on KDE overlap.

Table S2.F1. Results for the effects of boldness, sex, date, and colony on the overlap with colony-level kernel density estimation (95% KDE). Significant terms are indicated in bold. Two-way interactions between boldness and sex, and boldness and colony, were found to be non-significant and dropped from all models (results presented in the text). Estimates for sex effects are presented as the difference for males over females.

	Incubation			Chick rearing		
Predictor	Estimate ± SE	Test stat.	P value	Estimate ± SE	Test stat.	P value
Boldness	-0.02 ± 0.04	$F_{1,43} = 1.12$	0.73	-0.004 ± 0.04	$F_{1,47} = 0.02$	0.90
Sex (male)	0.02 ± 0.04	$F_{1,43} = 1.12$	0.73	0.013 ± 0.07	$F_{1,47} = 0.05$	0.83
Date	0.02 ± 0.04	$F_{1,43} = 0.29$	0.60	-0.056 ± 0.05	$F_{1,47} = 1.50$	0.23
Colony		$F_{3,45} = 9.77$	**< 0.001**		$F_{3,49} = 3.67$	**0.02**

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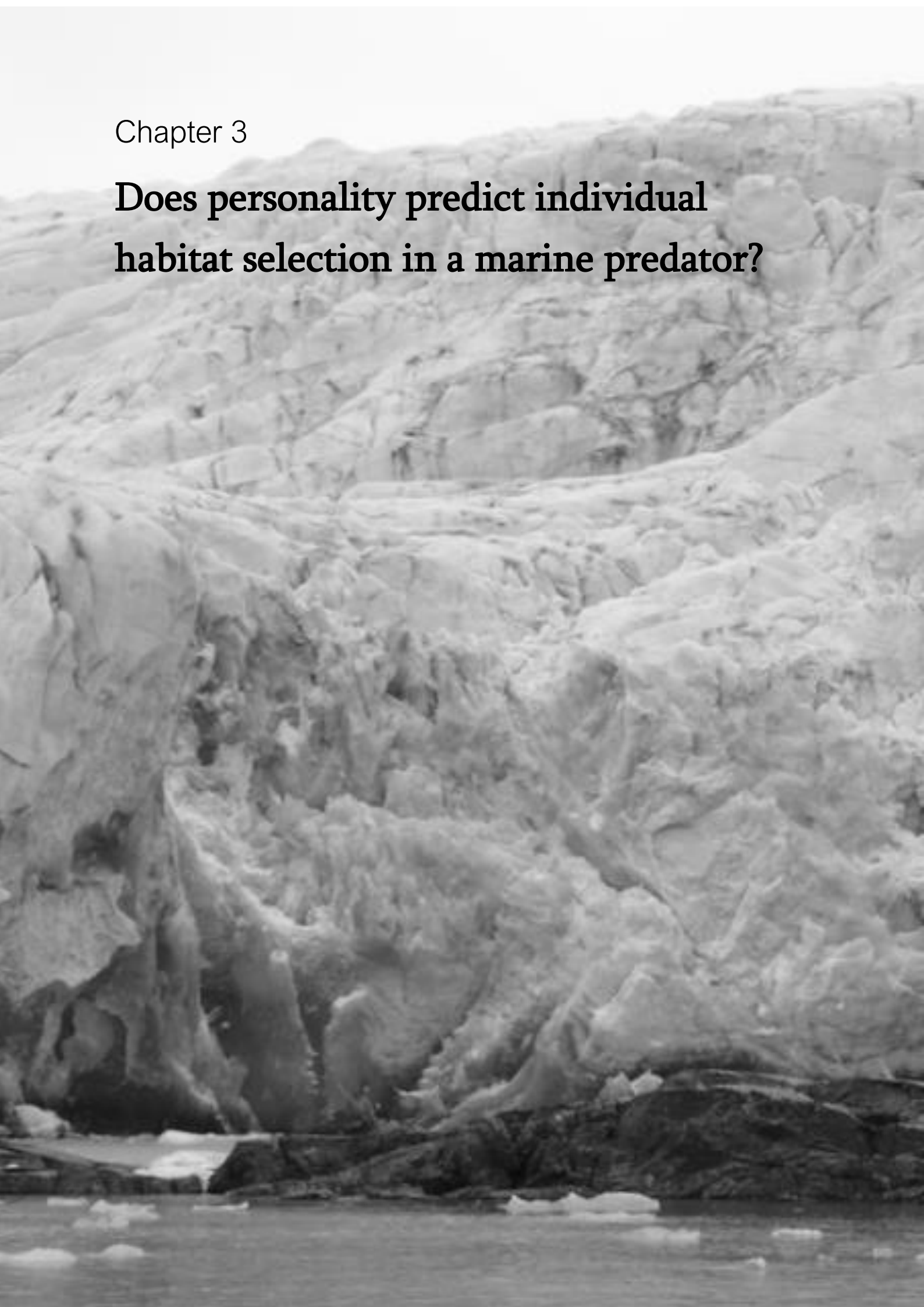
Chapter 3

Does personality predict individual habitat selection in a marine predator?



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Does personality predict individual habitat selection in a marine predator?

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Abstract

When choosing where to forage, animals should select the optimal habitat which maximises their resource gain while minimising the cost for their phenotype. An animal's personality is expected to strongly influence its foraging habitat selection; in particular, because boldness is associated with reduced flexibility in behaviour, bold individuals are expected to preferentially select for temporally predictable resources and be consistent in their habitat preferences, whilst shy individuals should rely more heavily upon unpredictable resources, and be more variable in their habitat selection. Here, we tracked the foraging movements and assessed the personality of black-legged kittiwakes (*Rissa tridactyla*) breeding at five colonies in Svalbard. Using resource selection functions, we then quantified individual differences in kittiwakes' habitat selection in relation to both static (predictable) and dynamic (unpredictable) drivers of seabird foraging habitat. We examined whether boldness predicted individuals' habitat selection and repeatability of habitat selection. Individual kittiwakes were highly repeatable in their habitat selection during the chick rearing phase of breeding, but not during incubation. Bold kittiwakes foraged preferentially in deeper waters during chick rearing, and males foraged in shallower regions during incubation, but much variation in habitat selection remains unexplained. We also found differences in the repeatability of habitat selection, with shy kittiwakes exhibiting low repeatability in their selection for static features during chick rearing, possibly linked to their low foraging site fidelity and tendency for flexible foraging behaviour. Our findings highlight the high levels of individual variability in habitat selection in marine predators, the drivers of which warrant further study to advance our understanding of population-level habitat selection patterns.

Keywords: habitat selection; boldness; phenotype-environment covariance; foraging specialisation; individual consistency; movement ecology; animal personality; repeatability

1.0 Introduction

Foraging animals must often select from a range of available habitats when deciding where to feed. The decision should be based upon the resources that each habitat offers, as well as the associated risk, with the optimal foraging habitat being that which minimises risk whilst maximising resource gain (MacArthur *et al.*, 1966; Stephens *et al.*, 1986). Because individuals differ in their resources requirements and behavioural responses to risk, we should expect individuals within populations to vary in their habitat selection, preferentially selecting the most optimal habitat for their phenotype (Rosenzweig, 1981; Bolnick *et al.*, 2003; Morris, 2011; Jacob *et al.*, 2015). Despite this, habitat selection has typically been examined as a feature of populations, implicitly assuming that individuals are ecologically equivalent (Piper, 2011). However, growing evidence supports that populations are comprised of individuals which vary greatly in their habitat preferences, often consistently over time, suggesting that individuals may be specialised in their habitat selection (Leclerc *et al.*, 2016; Lesmerises *et al.*, 2017; Trevail, 2019). This individual variation is of high importance for species conservation, because habitat loss and alteration will impact individuals unevenly depending on their preferences (Bolnick *et al.*, 2003; Dall *et al.*, 2004; Hendry, 2016). Understanding the phenotypic traits which shape habitat selection is therefore critical to understanding population responses to habitat alteration, especially for populations experiencing rapid rates of change.

An important source of phenotypic variation with potential to shape individuals' habitat selection is animal personality. Animal personalities are individual differences in fundamental behavioural traits that are consistent over time and across contexts (Gosling, 2001; Sih *et al.*, 2004; Réale *et al.*, 2007). Recent evidence suggests that individuals should be found in the habitats that best fit their personality (the "personality-matching hypothesis", Holtmann *et al.* 2017). Numerous studies have considered the effects of sex, age, morphological and physiological variation on foraging habitat selection (Polis, 1984; Bolnick *et al.*, 2003; Araújo *et al.*, 2011; Lesmerises *et al.*, 2017; Oliveira *et al.*, 2018). By contrast, whether personality influences the habitat in which individuals select to forage remains largely unexplored. This omission is surprising given that recent research has established strong influences of personality traits on foraging movements and space use (reviewed by: Toscano *et al.* 2016; Spiegel

et al. 2017). In particular, the bold-shy personality axis, which describes individuals' willingness to undertake risks (Dammhahn *et al.*, 2012), has been linked to foraging movement tendencies (Patrick *et al.*, 2014), feeding search patterns (Van Overveld *et al.*, 2010), and foraging site fidelity (Harris *et al.*, 2020). However, the potential for boldness to explain the habitats in which individuals forage has received less consideration.

Animals may partition their habitat usage by boldness via a number of mechanisms. Bold individuals are often of a higher competitive ability (Webster *et al.*, 2009; Rudin *et al.*, 2012), which may confer greater access to higher-quality feeding habitats (Holbrook *et al.*, 1992). A number of studies have also shown that bold individuals are more likely to occupy "riskier" habitats, such as in open areas away from refuge (Bonnot et al., 2015; Pearish et al., 2013; Wilson & McLaughlin, 2007) or in human-dominated spaces (Holtmann *et al.*, 2017). Additionally, bold and shy individuals may select for habitat features varying in predictability: bold animals are often characterised by rigid and routine-like behavioural tendencies, while shy animals are typically more behaviourally flexible and responsive to changes in the environment (Benus *et al.*, 1990; Wolf *et al.*, 2008; Coppens *et al.*, 2010; Ruiz-Gomez *et al.*, 2011; Villegas-Ríos *et al.*, 2018). When locating resources, bold animals are expected to rely more heavily upon previous knowledge of food availability, whereas shy animals should use information of the prevailing conditions, which may take time to acquire but provide more accurate cues of foraging opportunities (Verbeek *et al.*, 1994; Coppens *et al.*, 2010). In landscapes where resources vary in predictability, bold animals may therefore preferentially select for foraging habitats that are predictable over time, while shy animals are more likely to respond to transient cues of foraging opportunity. In the marine environment, resource distributions tend to be highly patchy and vary in predictability: local areas of productivity are generated by static oceanic features, such as bathymetric irregularities (e.g. shelf edges), but also by dynamic features that change over short timescales, such as sea surface temperature (SST) and ephemeral fronts (Hunt *et al.*, 1999; Hedd *et al.*, 2014). Accordingly, both predictable and unpredictable foraging habitats are available to marine predators (Weimerskirch, 2007; Urmy *et al.*, 2018), presenting an ideal opportunity to test whether bold and shy individuals differ in their selection for habitat features depending upon their predictability.

As well as varying in the habitats they select, individuals may also differ in the degree to which they are specialised in their habitat selection (Wilson *et al.*, 1994; Bolnick *et al.*, 2003). For example, populations of bluegill sunfish (*Lepomis macrochirus*) segregate into benthic specialists, limnetic specialists, or generalists using a mixture of the two (Werner *et al.*, 1981). Such variation may also be linked to personality differences: owing to their increased behavioural flexibility and responsiveness to environmental cues, shy individuals may vary greatly in their habitat selection decisions, depending on the environmental conditions of the moment, and therefore exhibit low repeatability in their habitat selection. Meanwhile, bold individuals may consistently forage in the same habitats owing to their rigidity in behaviour (Benus *et al.*, 1990; Wolf *et al.*, 2008; Coppens *et al.*, 2010). In support of this, in a previous study we found a higher degree of spatial specialisation in bold than shy individuals: bolder black-legged kittiwakes (*Rissa tridactyla*) were more repeatable in their foraging trips and showed higher site fidelity to previous foraging locations (Harris *et al.*, 2020). This spatial pattern could be driven by differences in habitat selection: if bolder kittiwakes select for predictable foraging habitats, while shy individuals use more spatially variable resources, differences in site fidelity may emerge. Additionally, bolder kittiwakes should exhibit higher repeatability in habitat selection than shy individuals, in keeping with their greater spatial consistency.

Here, we revisited the same study system of Arctic-breeding black-legged kittiwakes to examine whether boldness predicts (i) foraging habitat selection, and (ii) repeatability in foraging habitat selection. As central-place foragers during the breeding season, kittiwakes make wide-ranging trips of tens to hundreds of kilometres from their nest sites to forage, where they feed upon prey at the sea surface (Furness *et al.*, 2000; Coulson, 2011). Kittiwakes are known to make use of prey aggregations along bathymetric features such as shelf edges and seamounts (Chivers *et al.*, 2013; Christensen-Dalsgaard *et al.*, 2018), as well as dynamic SST gradients which correlate with many of their prey species (Frederiksen *et al.*, 2007; Robertson *et al.*, 2014). Additionally, in Arctic waters, tidewater glacier fronts constitute important foraging habitat for surface-feeders such as kittiwakes (Hartley *et al.*, 1936), as the discharge of melted freshwater promotes upwellings and create dense hotspots of prey at the sea surface (Lydersen *et al.*, 2014; Urbanski *et al.*, 2017).

We quantified kittiwake habitat selection in relation to three static environmental covariates (bathymetry, seabed slope, and glacier fronts), and one dynamic covariate (SST). To test for consistent individual differences in habitat selection, which may indicate individual specialisation (Bolnick *et al.*, 2002), we tested whether kittiwakes exhibit repeatability in their habitat selection. We then examined whether differences in habitat selection were explained by boldness, predicting that bold kittiwakes should select more strongly for static habitat features (bathymetry, seabed slope, glacier fronts), while shy individuals should rely upon dynamic features (SST). We also tested for differences in repeatability of habitat selection between bold and shy individuals, predicting that bolder kittiwakes should be more repeatable in their habitat selection than their shy conspecifics. Finally, because sex differences in foraging behaviour and habitat selection are also common in seabirds (Catry *et al.*, 2006; Phillips *et al.*, 2017), we also examined the effects of sex.

2.0 Methods

2.1 Study system

We carried out fieldwork during the breeding seasons of 2017 and 2018 at five kittiwake colonies on the west coast of Spitsbergen, Svalbard: Blomstrand (78°59′N 12°07′E; June-July 2017), Krykkjefjellet (78°53′N 12°11′E; June-July 2017) and Observasjonholmen (78°56′N 12°16′E; June-July 2017-2018) in Kongsfjorden, and Grumantbyen (78°10′N 15°05′E; June-July 2017-2018) and Pyramiden (78°39′N 16°19′E; June-July 2018) in Isfjorden. Adult kittiwakes were captured at their nests using a wire noose, whereupon they were fitted with a metal leg ring, measured (head-bill length was recorded to the nearest 0.1mm), and blood or feather samples were collected for sex determination. We identified the sex of most birds by molecular analysis of DNA, or, where genetic samples were unobtainable (N = 5), by morphometric assessment of head-bill length (Coulson 2009; see Appendix S3.A for full details of sexing methods).

2.2 Boldness tests

Boldness assays were conducted using a novel object test following the protocol described by Harris *et al.* (2020). Briefly, we tested boldness by measuring individuals'

responses to a novel object, presented to birds at the nest. A blue plastic penguin toy (dimensions 13 × 10 × 4.5 cm; Munchkin®), mounted on the end of a carbon fibre fishing pole, was presented at the nest for 60 seconds, with an action camera fixed behind the object filming the bird's response. We subsequently recorded the proportion of each test an individual spent in each of five mutually exclusive behavioural states: (1) sitting on the nest; (2) body lifted off the structure of the nest, but not standing; (3) standing on the nest, with legs visible and extending to the base of the nest; (4) off the nest but remaining on the cliff or window ledge beside the nest; (5) off the cliff or window ledge altogether (and no longer within view of the camera). We tested 191 individuals over two years: 116 individuals were tested once, 40 were tested twice, and 35 were tested three or more times. A Principal Component Analysis (PCA) was used to collapse the five behavioural variables into a single boldness test score (PC1; see Appendix S3.B for variable loadings), previously shown to be highly repeatable in kittiwakes (Harris *et al.*, 2020). We confirmed this repeatability using the *rptR* package (Stoffel *et al.*, 2017) to calculate adjusted repeatability of PC1 (repeatability after controlling for confounding effects; Nakagawa & Schielzeth 2010). As fixed effects, we included test date, breeding stage (incubation or chick rearing), and test number. Finally, we extracted a single estimate of boldness for each individual across all of its tests using a linear model, where PC1 was fitted as the response variable and individual ID, test date, breeding stage, and test number were fitted as fixed effects. As in our previous study (Harris *et al.*, 2020), we found no difference in boldness among the sexes (results from a linear model: $p = 0.24$, Appendix S3.A).

2.3 Quantifying foraging habitat selection

2.3.1 GPS tracking of foraging trips

We used GPS loggers to track the foraging movements of breeding kittiwakes during both incubation and chick rearing stages of breeding. GPS loggers (either i-gotU GT-120 loggers, Mobile Action©, or CatLog (Gen1 or Gen2) loggers, http://www.mr-lee.com/sc_supp.htm) were sealed in waterproof heat shrink tubing and attached to birds' back feathers using TESA tape. All loggers weighed <5% of a kittiwake's body mass; full details of sample sizes of logger types used are provided in Appendix S3.C. Logger mass did not affect habitat selection estimates (Appendix S3.C) We programmed loggers to record locations every 10-minutes on incubating birds and every 2-minutes

on chick-rearing birds, except at Krykkjefjellet, where loggers were programmed at a 10-minute resolution during chick rearing to meet the data requirements of another study. Birds were recaptured and loggers retrieved after 1 to 13 days, depending on the presence of the focal individual at the nest during our visits to the colony.

2.3.2 Identification of foraging locations

We fitted a 300m buffer around each colony, and considered departures from this buffer greater than one hour as foraging trips (based on the frequency distributions of point distance to the colony, and trip durations, respectively). We also visually inspected all trips for evidence of detectable foraging movements (characterised by reduced speed and increased tortuosity, or area-restricted search (ARS); Fauchald & Tveraa 2003). 82 trips (14%) contained no evidence of ARS, and were consequently removed from analyses. These trips were considerably shorter than the mean trip duration (2 hours, versus 11 hours) and tended to terminate on land, supporting that these departures from the colony were for purposes besides foraging, such as freshwater bathing. Tracks were linearly interpolated to intervals of 10 minutes during incubation and 2 minutes during chick rearing using adehabitatLT (Calenge, 2015), in order to standardise data resolution and account for occasional missing data points.

To identify locations of foraging activity during trips, we used hidden Markov models (HMMs) to classify behaviour at each GPS point as either foraging, resting, or travelling. HMMs were fitted using the *moveHMM* package (Michelot *et al.*, 2016), and classifications were made based upon the distributions of step lengths and turning angles between consecutive GPS points. Separate HMMs were run for each breeding stage (incubation and chick rearing) and for each fjord (Isfjorden and Kongsfjorden) owing to differences in the distributions of step lengths and turning angles, resulting in four HMMs in total. Starting parameters were informed by previous classification of kittiwake at-sea behaviour (Harris *et al.*, 2020) and are provided in supplementary material Appendix S3.D. Foraging points more than 500m inland of the coastline were removed (based on the frequency histogram of distance to the coastline for all foraging points over land), as these are likely to indicate commuting behaviour and cannot represent foraging activity. Points less than 500m inland were retained to account for error in GPS fixes or coarseness of the coastline, particularly at glacier fronts. In total, we recorded 31,166

foraging locations, 7,547 during incubation (from 151 trips, by 67 individuals) and 23,619 during chick rearing (from 259 trips, by 70 individuals). A number of individuals were tracked during both breeding stages and both years.

2.3.3 Assessment of available habitat

We assessed kittiwake habitat selection in relation to four environmental covariates using resource selection functions (Manly et al. 2002). Resource selection functions compare environmental characteristics of "used" habitat (here, kittiwakes foraging locations) with that of the "available" habitat (where kittiwakes could potentially forage). To represent the foraging habitat available to kittiwakes, we first calculated maximum foraging ranges specific to each colony, year, and breeding stage (range: 22.81-525.42km; all ranges provided in supplementary material Table S3.E1). For each used foraging location, we randomly sampled two corresponding "available" locations from within the relevant foraging radius. The ratio of 2:1 available to used locations was determined by running models with between one and ten available points, and selecting the lowest number that yielded accurate slope estimates (Appendix S3.E), following (Trevail, 2019). The same available locations were used for all four environmental covariates.

2.3.4 Environmental covariates

We examined kittiwake habitat selection in relation to four environmental covariates known to influence Arctic seabird foraging distributions: (1) bathymetry (sea floor depth); (2) seabed slope; (3) presence at a tidewater glacier front (binary); (4) sea surface temperature (SST). These covariates were selected on the basis of their influence on seabird foraging; full rationale for the inclusion of each covariate, and details of data sources, are provided in Table 3.1. Covariates were extracted for each kittiwake foraging location and two corresponding available locations. For glacier fronts, we measured the minimum distance between all locations and the nearest tidewater glacier front using the *gDistance()* function of the *rgeos* package (Bivand *et al.*, 2018), and coded locations 1 when they were within 500m of a glacier front (indicating foraging at the glacier front) and otherwise as 0.

Table 3.1. Details of the environmental covariates examined in resource selection functions as drivers of kittiwake habitat selection, including data resolution (spatial, and temporal for SST), transformations applied to approach a normal distribution (separated by breeding stage: incubation vs. chick rearing), rationale for their inclusion, and data source.

Type	Environmental covariate	Source	Data resolution	Transformation		Rationale for inclusion
				Inc.	Chi.	
Static	Bathymetry (m)	Extracted from the 2019 General Bathymetric Chart of the Oceans (GEBCO).	15 arc-seconds	√	log	Predicts distributions of a number of important prey species for kittiwakes (Hop *et al.*, 2013; Astthorsson, 2016). Bathymetric features often associated with aggregations of marine predators including seabirds (Yen *et al.*, 2004).
Static	Seabed slope (°)	Estimated from GEBCO data using the terrain() function from the raster package (Hijmans, 2017) in R.	15 arc-seconds	log	log	Steep seabed slopes (e.g. at shelf breaks and continental shelves) modify water fluxes which can concentrate prey, and in turn, drive aggregations of marine predators, including kittiwakes (Chivers et al. 2013; Wakefield et al. 2017; Christensen-Dalsgaard et al. 2018).
Static	Glacier fronts	Foraging locations within a 500m buffer of glacier fronts classified as 1, otherwise 0. Glacier front shapefiles provided by Geir Moholdt.	N/A (binary)	NA	NA	Freshwater discharged by melting glaciers promotes upwellings of prey paralysed by osmotic shock (Węsławski *et al.*, 1998, 2000), which produces dense foraging hotspots used by Arctic seabirds, including, notably, kittiwakes (Lydersen *et al.*, 2014; Urbanski *et al.*, 2017).
Dynamic	SST (°C)	Extracted from the NASA OceanColor website using data from the MODIS Aqua satellite.	8 days/ 4km	none	none	Indicative of processes which shape prey distributions, often correlated with seabird foraging distributions (Schneider, 1990; Frederiksen *et al.*, 2007; Carroll *et al.*, 2015; Van Eeden *et al.*, 2016).

Bathymetry data were unavailable for 9% of locations due to a coarse data resolution along coastlines. For these locations, we estimated bathymetry by bilinear interpolation within a buffer of 1.3km, which was sufficient to provide bathymetry data for all locations. SST data were unavailable for 13% of locations due to gaps in MODIS Aqua data because of cloud cover. To obtain accurate estimates of SST for these locations, we estimated SST by bilinear interpolation within a buffer of initially 1km, and where SST data were still unavailable, we increased this buffer by stepwise increments of 1km up to a maximum of 10km (see Appendix S3.F for validation), in order to maximise SST data coverage. This was sufficient to provide SST data for 98% of locations, and the remaining 2% of locations for which SST could not be accurately estimated were removed. In order to maintain a constant ratio of 2:1 available to used locations, we retained locations only where environmental covariates could be extracted at the used location and both corresponding available locations, resulting in a final dataset of 29,487 foraging locations for SST models (6,220 during incubation, from 151 trips by 67 individuals; 23,267 during chick rearing, from 259 trips by 70 individuals), while all foraging locations (N = 31,166) were retained for bathymetry, seabed slope, and glacier front models. Environmental data are plotted in Figure 3.1, with foraging locations in Figure 3.1a.

Prior to fitting resource selection functions, we assessed relationships among continuous environmental covariates using Spearman's rank correlations (see Appendix S3.F). Bathymetry at extracted locations was positively correlated with seabed slope ($R = 0.25$, $p < 0.001$) and negatively correlated with SST ($R = -0.20$, $p < 0.001$); seabed slope and SST were positively correlated ($R = 0.18$, $p < 0.001$). We were still able to examine selection in relation to each covariate without encountering multicollinearity issues as environmental covariates were each fitted in separate habitat selection models.

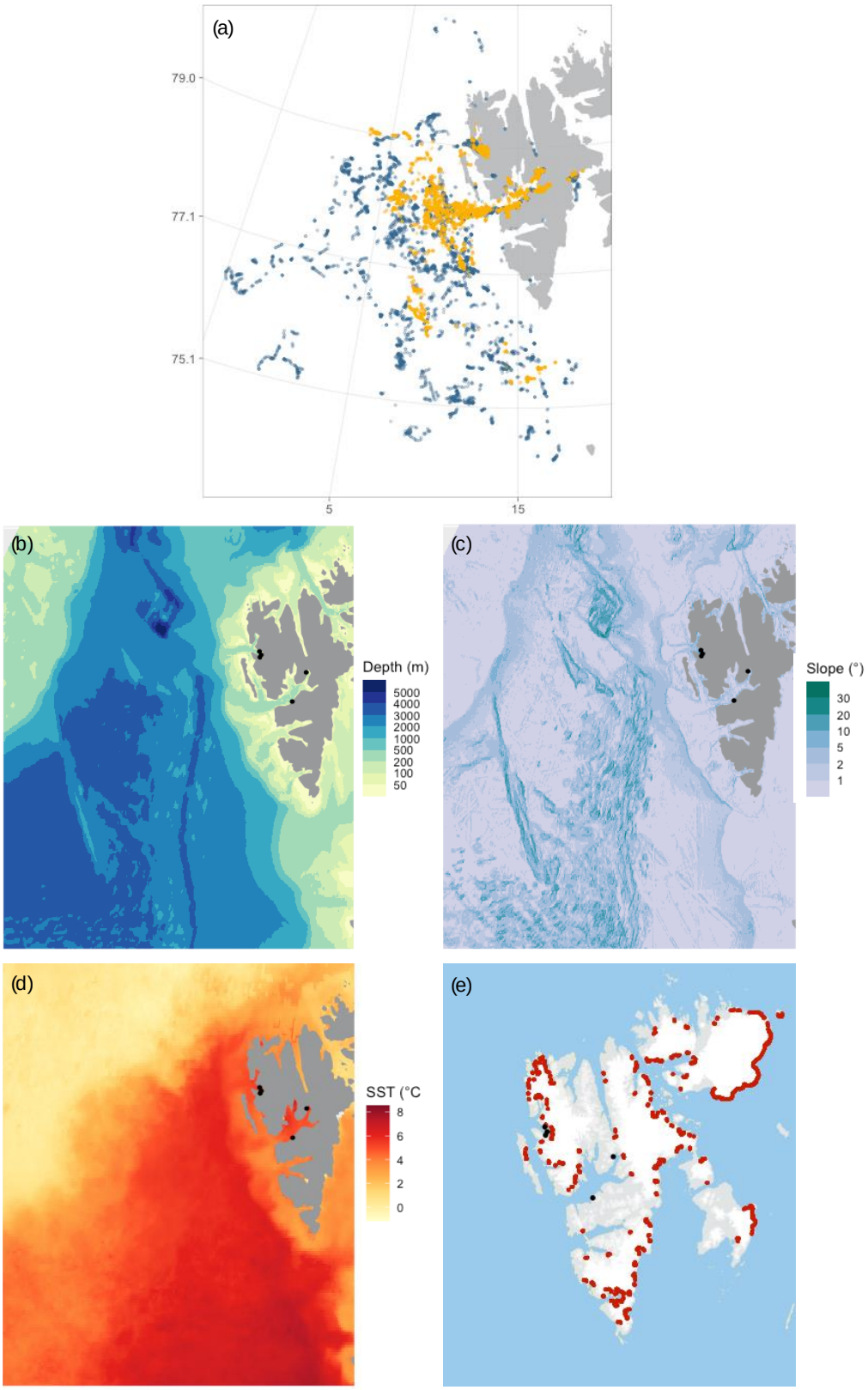

Figure 3.1. Study area in Svalbard showing (a) kittiwake foraging locations (blue: incubation; yellow: chick rearing) and (b-e) environmental covariates: (b) bathymetry; (c) seabed slope; (d) SST (averaged over June-July 2017 and 2018); (e) locations of tidewater glacier fronts around the Svalbard coast (in red). Colony locations are marked in black.

2.3.5 Resource selection functions

Resource selection functions were fitted as binomial logistic mixed effects models in the *lme4* package (Bates *et al.*, 2015). Selection was fitted as the binomial response variable, coded 1 for used habitat (kittiwake foraging locations) and 0 for available locations. We fitted one model for each of the four environmental covariates during each breeding stage (incubation and chick rearing), resulting in eight models in total, with the relevant environmental covariate fitted as a fixed effect in each model. In all models, we additionally included as fixed effects year, colony, and distance between the location and the colony. The latter variable was included to account for the fact that central place foragers tend to forage preferentially close to their nest sites (Matthiopoulos, 2003; Chivers *et al.*, 2013), and so foraging locations are more likely to be clustered close to the colony than at the edge of an animal's maximum foraging range. We applied transformations to environmental covariates and distance to the colony where necessary, based upon the distribution of residuals (transformations are detailed in Table 3.1).

Locations were weighted to account for the 2:1 ratio of available to used locations, as this has been shown to improve the accuracy of model predictions (Barbet-Massin *et al.*, 2012). For each model, we evaluated the inclusion of fixed effects using the Akaike Information Criterion (AIC) to compare models with and without the relevant effect. The model with the lowest ΔAIC values was retained as the "best" model (Burnham *et al.*, 2007). In all cases, the maximal model (including all covariates) was retained (see Results). All continuously distributed covariates were scaled (mean = 0, variance = 1) to facilitate model fitting and interpretation of parameter estimates. We fitted random slopes and intercepts at the trip level, where each trip ID was unique to bird ID. Trip-level random slopes were then extracted from resource selection functions as habitat selection estimates for each trip (Courbin *et al.*, 2018; Muff *et al.*, 2020). Global slope estimates were extracted from each model as estimates of habitat selection at the population level (across all individuals from all colonies). Slopes below zero indicate selection for lower environmental values than the average available (e.g. lower temperatures), while slopes greater than zero indicate selection for higher environmental values than the average available (e.g. higher temperatures).

2.4 Statistical analyses

Data preparation and analysis was conducted in R version 3.5.1 (R Core Team, 2018). As not all personality tested kittiwakes were GPS tracked, and not all GPS tracked kittiwakes were personality tested, analyses were based on a sample size of 65 individuals during incubation and 62 individuals during chick rearing (103 unique individuals in total, as some individuals were tracked during both breeding stages and/or in multiple years).

2.4.1 Intrinsic predictors of habitat selection preferences

We investigated whether habitat selection estimates were linked to differences in boldness and sex using linear mixed effects models. Trip-level habitat selection estimates (i.e. random slopes) were fitted as the response variable, with boldness, sex, and their two-way interaction fitted as fixed effects, and individual ID fitted as a random intercept to control for multiple observations per individual. Separate models were fitted for each covariate and each breeding stage (eight models in total).

2.4.2 Repeatability of habitat selection

We estimated repeatability of habitat selection estimates using the *rptR* package (as per Courbin et al., 2018; Leclerc et al., 2016). Repeatability is bounded between 0 and 1, where higher values indicate that individual ID explains a large proportion of variation in habitat selection, and therefore that individuals are consistent in their habitat selection. We first calculated repeatability, separately for each environmental variable and breeding stage, for all individuals collectively, to test whether kittiwakes exhibited consistent individual differences in habitat selection. We then tested for differences in repeatability associated with boldness and sex by comparing repeatability among (i) bold versus shy kittiwakes, and (ii) males versus females. For the purpose of this analysis only, boldness was treated as a categorical variable rather than a continuous measure, in order to compare repeatability among the two groups. Kittiwakes were categorised as either "bold" (higher boldness scores) or "shy" (lower boldness scores) based upon the median boldness score. We checked for non-overlapping 84% confidence intervals as an indication of significant differences in repeatability between groups, since the absence of overlapping 84% confidence intervals is equivalent to a z-test at the 0.05 level (Tryon, 2001; Payton *et al.*, 2003; Aplin *et al.*, 2015).

Table 3.2. Kittiwake habitat selection, during incubation and chick rearing, in relation to four environmental covariates. ΔAIC denotes the improvement in AIC by adding the relevant environmental covariate to the model. Population-level selection estimates are the global slopes extracted from resource selection functions (positive estimates indicate selection for an environmental variable; negative estimates indicate avoidance). Repeatability was calculated from trip-level random slopes extracted from resource selection functions with random slopes and intercepts fitted at the foraging trip-level. We present repeatability estimates for all individuals collectively (repeatability of habitat selection), as well as repeatability estimates for bold and shy, male and female kittiwakes, in order to contrast repeatability among groups. Group-level estimates are highlighted in bold where 84% confidence intervals (in square brackets) are non-overlapping, indicating a difference between two groups (i.e. between bold and shy, or male and female).

	Environmental covariate	ΔAIC effect of covariate	Population-level selection estimates (± s.e.)	Repeatability of selection (± s.e.)	Comparison of repeatability among groups [84% CI]			
					Bold	Shy	Male	Female
Incubation	Bathymetry	7,102	Negative (-2.13 ± 0.35)	R = 0.01 ± 0.08 p = 0.47	**R = 0.00 [0.00, 0.00]**	**R = 0.10 [0.07, 0.14]**	**R = 0.18 [0.13, 0.23]**	**R = 0.00 [0.00, 0.00]**
	Seabed slope	1,462	Positive (0.29 ± 0.05)	R = 0.00 ± 0.07 p = 1.00	**R = 0.00 [0.00, 0.00]**	**R = 0.05 [0.04, 0.07]**	**R = 0.42 [0.33, 0.51]**	**R = 0.00 [0.00, 0.00]**
	Glacier fronts	6,282	Positive (3.85 ± 0.81)	R = 0.00 ± 0.14 p = 1.00	R = 0.00 [0.00, 0.00]	R = 0.00 [0.00, 0.00]	R = 0.00 [0.00, 0.00]	R = 0.00 [0.00, 0.00]
	SST	259	Positive (2.48 ± 0.18)	R = 0.08 ± 0.09 p = 1.00	**R = 0.00 [0.00, 0.00]**	**R = 0.04 [0.03, 0.05]**	**R = 0.02 [0.01, 0.03]**	**R = 0.00 [0.00, 0.00]**
Chick rearing	Bathymetry	17,174	Negative (-0.49 ± 0.12)	R = 0.29 ± 0.07 **p < 0.001**	**R = 0.58 [0.50, 0.64]**	**R = 0.04 [0.03, 0.05]**	R = 0.39 [0.30, 0.46]	R = 0.29 [0.22, 0.36]
	Seabed slope	17,105	Negative (-0.75 ± 0.10)	R = 0.43 ± 0.07 **p < 0.001**	R = 0.45 [0.36, 0.51]	R = 0.38 [0.30, 0.44]	R = 0.34 [0.26, 0.41]	R = 0.42 [0.34, 0.48]
	Glacier fronts	18,387	Positive (4.78 ± 0.30)	R = 0.37 ± 0.08 **p < 0.001**	**R = 0.66 [0.59, 0.71]**	**R = 0.13 [0.09, 0.17]**	R = 0.40 [0.31, 0.46]	R = 0.36 [0.28, 0.43]
	SST	16,798	Negative (-3.70 ± 0.79)	R = 0.46 ± 0.07 **p < 0.001**	R = 0.47 [0.40, 0.53]	R = 0.47 [0.40, 0.52]	**R = 0.39 [0.33, 0.46]**	**R = 0.54 [0.48, 0.60]**

3.0 Results

3.1 Boldness scores

Boldness scores were similarly repeatable to our findings reported in a previous study (Harris et al. 2020). PC1 explained 57.3% of the variation in response to the novel object test, and individuals were highly repeatable in their responses to the test over the two years of study ($R = 0.55$ [CI: 0.45, 0.65]; $p < 0.001$). Low values indicated "shy" responses and high values indicated "bold" responses, with scores ranging from -2.20 to 1.55.

3.2 Foraging trips

We recorded a total of 410 foraging trips, averaging 2.23 ± 1.42 trips per bird during incubation (mean ± SD; ranging from 1 to 10 trips), and 3.89 ± 2.86 trips per bird during chick rearing (range: 1 to 16). Kittiwakes made trips ranging up to 515km from the colony during incubation (mean ± SD foraging trip range: 97 ± 142km), and up to 301km from the colony during chick rearing (35 ± 52km). Colony- and year-specific maximum foraging ranges are reported in Appendix S3.E.

3.3 Population-level habitat selection

Environmental covariates improved the fit of resource selection functions in all cases ($\Delta AIC > 259$ for all models; Table 3.2), supporting that these covariates describe important foraging habitat characteristics for kittiwakes. Population-level estimates indicated kittiwakes foraged in areas characterised by shallower depths and preferentially at glacier fronts during both breeding stages (Table 3.2); meanwhile, selection with respect to seabed slope and SST appeared to shift between breeding stages, with kittiwakes foraging where slopes were steeper and in relatively warmer waters during incubation, but avoiding such areas during chick rearing (Table 3.2).

3.4 Individual-level habitat selection

At the individual level, kittiwakes varied greatly in the direction and strength of habitat selection, with covariates selected for by some individuals and avoided by others (Figure 3.2). With respect to SST, for example, models indicated that at the population level, kittiwakes shifted from using relatively warmer waters during incubation to cooler waters during chick rearing (Table 3.2); however, this appeared to be driven by a small

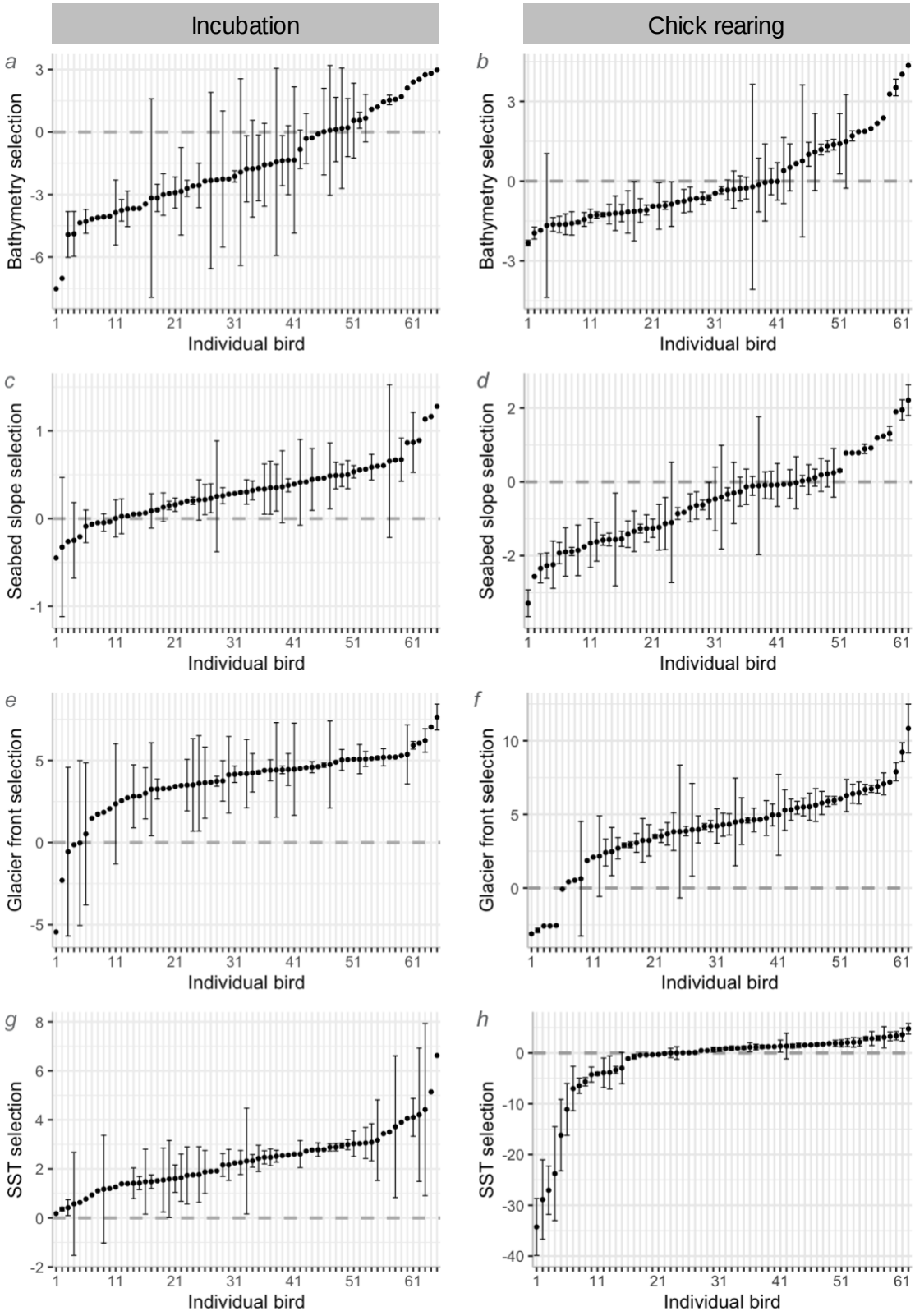

Figure 3.2. Estimates of habitat selection for each environmental covariate plotted by individual bird, where points indicate individuals' mean selection estimates across all foraging trips, with standard error bars for individuals for which multiple trips were recorded. For plotting purposes, birds are ranked in increasing order of selection estimate for each respective environmental covariate. Results are separated into selection during incubation foraging trips (left) and chick rearing foraging trips (right).

number of individuals strongly selecting for relatively colder areas during chick rearing, while the majority of kittiwakes continued to selectively forage in warmer waters (Figure 3.2h). Indeed, we detected individuals with opposing selection preferences (individuals with both positive and negative selection estimates, with errors not crossing zero) in five of eight habitat selection models (bathymetry during both breeding stages, Figure 3.2a-b; seabed slope during chick rearing, Figure 3.2d; glacier fronts during chick rearing, Figure 3.2f; SST during chick rearing, Figure 3.2h), indicating high individual variability in habitat selection in kittiwakes.

3.5 Predictors of individual habitat selection

Bolder kittiwakes selected deeper foraging areas than shy individuals during the chick rearing period (Table 3.3, Figure 3.3), although not during incubation. Males foraged in shallower regions during incubation (Table 3.3, Figure 3.4), but not during chick rearing. Habitat selection estimates for other covariates were otherwise not predicted by boldness, sex, or their two-way interaction (Table 3.3).

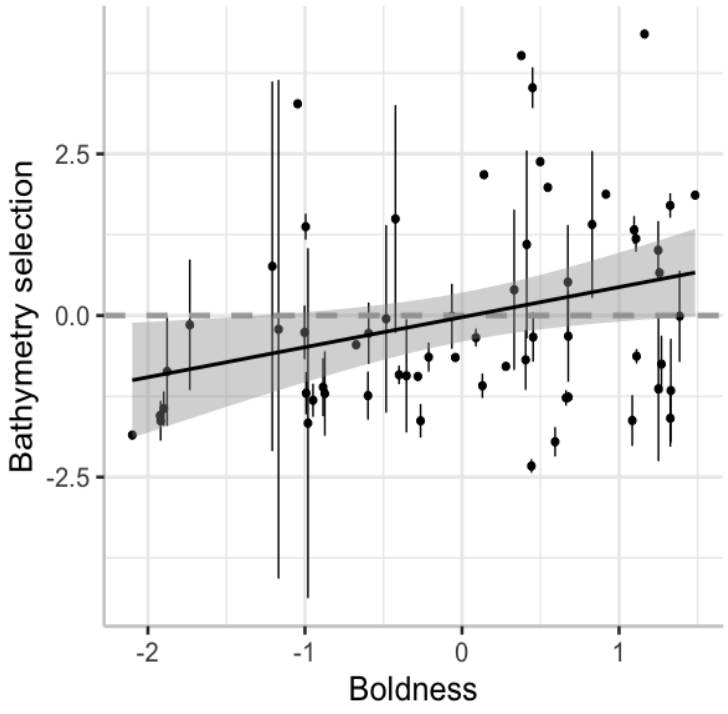

Figure 3.3. The relationship between boldness and estimates of selection for bathymetry during chick rearing. Positive values of bathymetry selection indicate selection for deeper waters, whereas negative values indicate selection for shallower waters. Error bars indicate standard errors in individuals' habitat selection over multiple trips.

Table 3.3. Effects of intrinsic variables (boldness, sex, and their interaction) on kittiwake habitat selection during incubation and chick rearing. Estimates for sex effects are presented as the difference for males over females. Significant terms are indicated in bold.

	Model and covariate	Estimate ± SE	Test statistic	p-value
Incubation	Bathymetry			
	Boldness	0.13 ± 0.25	$X^2_{(1,64)}$ = 0.27	0.61
	Sex (male)	-1.70 ± 0.51	$X^2_{(1,64)}$ = 10.82	**0.001**
	Boldness x sex (male)	-0.08 ± 0.56	$X^2_{(1,64)}$ = 0.02	0.89
	Seabed slope			
	Boldness	0.02 ± 0.04	$X^2_{(1,64)}$ = 0.18	0.67
	Sex (male)	-0.02 ± 0.08	$X^2_{(1,64)}$ = 0.05	0.82
	Boldness x sex (male)	0.16 ± 0.08	$X^2_{(1,64)}$ = 3.77	0.05
	Glacier fronts			
	Boldness	0.07 ± 0.24	$X^2_{(1,64)}$ = 0.09	0.77
	Sex (male)	0.89 ± 0.49	$X^2_{(1,64)}$ = 3.39	0.07
	Boldness x sex (male)	-0.10 ± 0.54	$X^2_{(1,64)}$ = 0.04	0.85
	SST			
	Boldness	0.05 ± 0.14	$X^2_{(1,64)}$ = 0.14	0.71
	Sex (male)	0.09 ± 0.28	$X^2_{(1,64)}$ = 0.10	0.75
	Boldness x sex (male)	0.32 ± 0.31	$X^2_{(1,64)}$ = 1.11	0.29
Chick rearing	Bathymetry			
	Boldness	0.39 ± 0.16	$X^2_{(1,61)}$ = 5.63	**0.02**
	Sex (male)	-0.09 ± 0.33	$X^2_{(1,61)}$ = 0.07	0.79
	Boldness x sex (male)	-0.06 ± 0.33	$X^2_{(1,61)}$ = 0.19	0.84
	Seabed slope			
	Boldness	0.10 ± 0.20	$X^2_{(1,61)}$ = 0.55	0.46
	Sex (male)	0.33 ± 0.29	$X^2_{(1,61)}$ = 1.39	0.24
	Boldness x sex (male)	-0.41 ± 0.29	$X^2_{(1,61)}$ = 2.20	0.14
	Glacier fronts			
	Boldness	-0.19 ± 0.31	$X^2_{(1,61)}$ = 2.98	0.08
	Sex (male)	-1.03 ± 0.61	$X^2_{(1,61)}$ = 0.37	0.55
	Boldness x sex (male)	0.20 ± 0.62	$X^2_{(1,61)}$ = 0.12	0.73
	SST			
	Boldness	0.05 ± 0.06	$X^2_{(1,61)}$ = 0.69	0.41
	Sex (male)	-0.03 ± 0.12	$X^2_{(1,61)}$ = 0.08	0.78
	Boldness x sex (male)	-0.04 ± 0.11	$X^2_{(1,61)}$ = 0.15	0.70

3.6 Repeatability in habitat selection

Repeatability of habitat selection was close or equal to zero during incubation (Table 3.2). By contrast, kittiwakes showed moderate to high repeatability in their habitat selection with respect to all covariates during chick rearing, with R values ranging from 0.29 ± 0.07 (for bathymetry) to 0.46 ± 0.07 (for SST), indicating individuals showed consistency in their use of foraging habitat characteristics (Table 3.2).

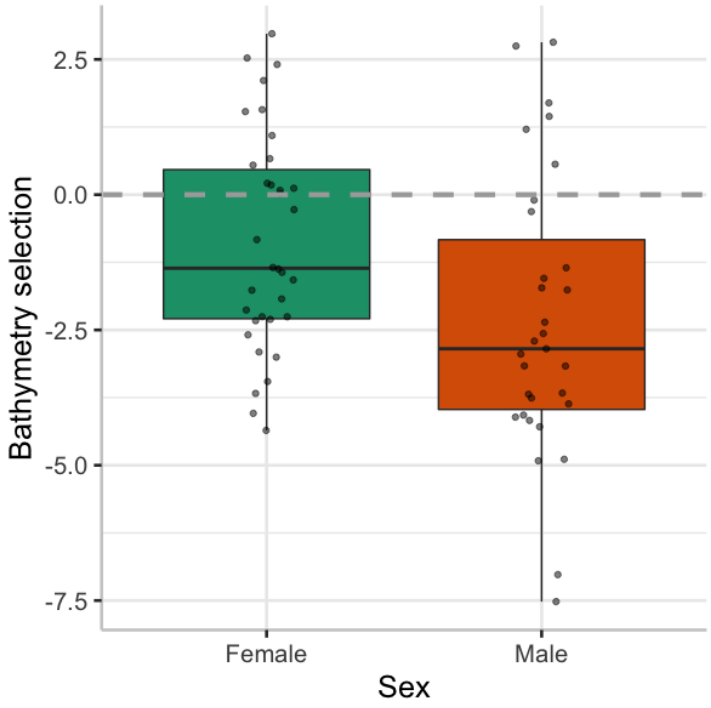

Figure 3.4. Sex differences in individual habitat selection estimates in relation to bathymetry during incubation.

3.7 Predictors of repeatability in habitat selection

We found differences in repeatability linked to both boldness and sex (Figure 3.5; Table 3.2). During incubation, repeatability estimates for bathymetry, seabed slope and SST were slightly higher for shy than bold kittiwakes (Table 3.2), but all estimates for both groups were equal or close to zero (Table 3.2, Figure 3.5a). While bold kittiwakes showed high repeatability in their usage of bathymetry and glacier fronts during chick rearing, shy individuals showed low to no repeatability (Table 3.2, Figure 3.5b). Bold and shy individuals exhibited similarly high levels of repeatability in their selection for seabed slope and SST (Table 3.2, Figure 3.5b).

Males were more repeatable than females in their selection for bathymetry and seabed slope during incubation (Table 3.2, Figure 3.5c), while for glacier fronts and SST, repeatability was close to zero for both sexes (Table 3.2). During chick rearing, males and females exhibited similarly high levels of repeatability for all bathymetry, seabed slope, and glacier fronts, while females were more repeatable in their selection for SST than males (Table 3.2, Figure 3.5d).

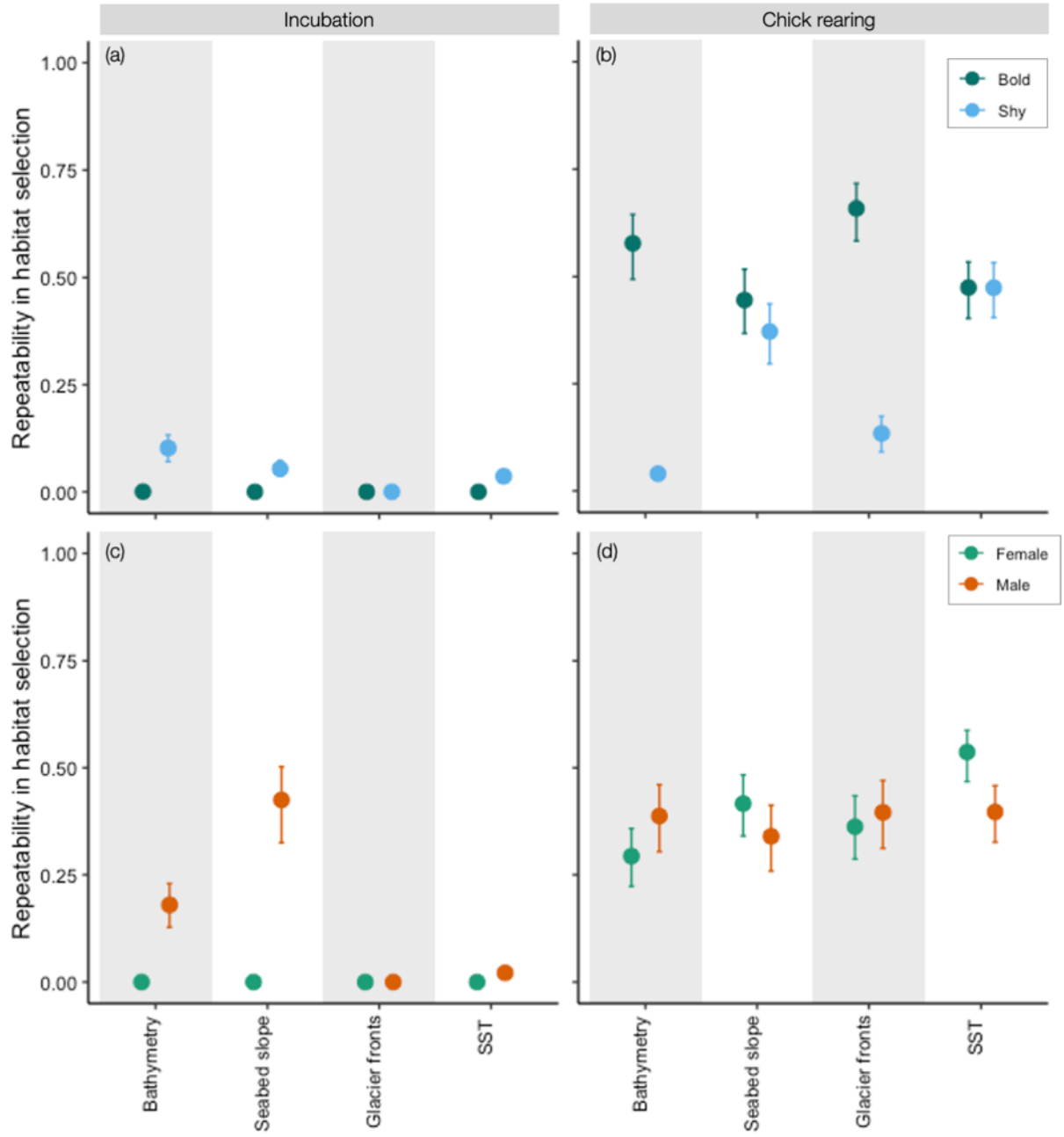

Figure 3.5. Differences in repeatability of habitat selection between bold and shy kittiwakes (upper panels) and between male and female kittiwakes (lower panels), with respect to four environmental covariates. Habitat selection estimates are separated into selection during incubation foraging trips (a, c) and chick rearing foraging trips (b, d). 84% confidence intervals are displayed.

4.0 Discussion

An individual's preferred habitat is expected to depend upon aspects of its phenotype (Bolnick *et al.*, 2003; Morris, 2011; Jacob *et al.*, 2015), yet most studies on habitat

selection report patterns only at the population level. Furthermore, few studies have explored how habitat selection is shaped by intrinsic factors beyond age and sex. Here, we applied a resource selection function approach to quantify the habitat selection preferences of individual kittiwakes foraging in the High Arctic, revealing consistent individual differences in habitat selection during chick rearing. Selection for bathymetry was linked to intrinsic factors, with bolder kittiwakes foraging in deeper regions than shy individuals during chick rearing, and males preferring shallower waters during incubation, but much variation in habitat selection remained unexplained. Bold and shy kittiwakes also differed in their consistency of habitat selection during chick rearing, with bolder individuals being highly repeatable in their selection for all environmental covariates, while shy individuals were not repeatable in their use of bathymetry and glacier fronts. These results demonstrate high levels of individual variability in habitat selection, which can partly be accounted for by the intrinsic factors of boldness and sex.

4.1 Habitat selection by kittiwakes

Our models identified important habitat drivers of kittiwake foraging at the population level. Across the breeding season, kittiwakes foraged preferentially in shallower waters and at glacier fronts. Glacier fronts constituted the most strongly selected for habitat feature during both incubation and chick rearing (Table 3.2), emphasising that glacier fronts represent key foraging areas for seabirds in Svalbard, as previously noted (Lydersen *et al.*, 2014; Urbanski *et al.*, 2017). During incubation, kittiwakes selected for areas where the seabed was steeper, but for flatter seabed areas during chick rearing. Breeding seabirds become particularly constrained in their foraging ranges post-hatching, when the nutritional requirements of their chicks necessitate feeding at frequent intervals (Ricklefs, 1983). Areas of steep bathymetric relief targeted by kittiwakes in Svalbard, such as the continental shelf break approximately 80km to the west (Christensen-Dalsgaard *et al.*, 2018), may fall out of range during chick rearing, such that kittiwakes are restricted to forage in flatter regions. Finally, kittiwakes also exhibited strong selection for relatively warmer sea surface temperatures during incubation, but cooler waters during chick rearing. Seabirds often forage in patches of cold water, likely linked to processes that enhance local productivity such as upwelling zones (Schneider, 1990; Robertson *et al.*, 2014; Carroll *et al.*, 2015; Van Eeden *et al.*, 2016). Selection for relatively warmer waters may correspond to inflowing warm

Atlantic currents, which bring Atlantic prey species into the waters west of Svalbard (Blanchet *et al.*, 2015; Vihtakari *et al.*, 2018).

Kittiwakes exhibited high repeatability in their habitat selection during the chick rearing period, but not during incubation. High repeatability may be indicative of individual specialisation (Bolnick *et al.*, 2002; Leclerc *et al.*, 2016; Courbin *et al.*, 2018). Individual foraging specialisations are highly prevalent in seabirds (Ceia *et al.*, 2015; Carneiro *et al.*, 2017), because they face high intraspecific resource competition and relatively predictable resource distributions, which collectively promote the partitioning of resources and consistent usage of foraging sites, behaviours, or habitats (Bolnick *et al.*, 2003; Araújo *et al.*, 2011). We previously found that kittiwakes' foraging trips are more repeatable in length, duration and range during the chick rearing period (Harris *et al.*, 2020), and suggest that this increased repeatability may be linked to reductions in trip length post-hatching, which restricts the range of habitats that birds can forage in, and thereby intensifies competition for resources.

4.2 Intrinsic predictors of variation in habitat selection

Boldness affected selection for bathymetry during chick rearing, with bolder kittiwakes foraging in deeper waters than shy individuals. Bolder animals are expected to exhibit a greater reliance upon previous knowledge of resource availability (Verbeek *et al.*, 1994; Coppens *et al.*, 2010), and may therefore select for regions of deeper waters as these can generate highly predictable foraging hotspots for seabirds (e.g. Urmy & Warren 2018). However, we found no evidence of boldness-dependent selection for other static habitat features of seabed slope and glacier fronts. Personality-specific habitat selection may reflect different dietary specialisations among bold and shy individuals (reviewed in Toscano *et al.* 2016), particularly if certain key prey species are found in particular habitats. Kittiwakes in Svalbard are known to feed on a broad range of prey, including mesopelagic species (Vihtakari *et al.*, 2018), which are likely to be associated with exclusively deeper waters, and could be preferentially selected by bold birds. Boldness correlates positively with energetic requirements in many species (Careau *et al.*, 2008, 2012; Réale *et al.*, 2010), which could drive segregation in prey preferences, and by extension, habitat selection (Toscano *et al.*, 2016). Future work should examine whether the foraging behaviour of bold and shy kittiwakes are associated with dietary

differences. Boldness-specific habitat segregation is also often ascribed to individual variation in the willingness to enter habitats perceived as "risky", such as where shelter from predators is lacking (Pearish *et al.*, 2013; Bonnot *et al.*, 2015). Adult kittiwakes do not face high predation risk at sea (Andersson, 1976), but risk of agonistic competitive interactions is likely to be higher in habitats associated with predictable foraging hotspots, and inferior competitors may actively avoid foraging hotspots for this reason (Cosner *et al.*, 1999; Anderson, 2010; López-Bao *et al.*, 2011).

In a previous study, we showed that bold kittiwakes exhibited higher foraging site fidelity during the breeding season (Harris *et al.*, 2020). We suggested that one driver of this relationship may be that bold individuals forage for more spatiotemporally predictable resources where intraspecific competition may be higher, such as prey-dense hotspots located at tidewater glacier fronts, while shy individuals track more ephemeral cues of foraging hotspots, such as SST gradients. However, we find no evidence that bold kittiwakes use glacier fronts more than shy individuals, nor that shy individuals select for specific SST. This suggests that other mechanisms besides habitat preference link boldness to site fidelity, such as greater variability in foraging behaviour among shy individuals (Verbeek *et al.*, 1994). Alternatively, personality-dependent foraging habitat selection may occur and lead to differences in site fidelity, but for habitat features beyond those examined here. The dynamic habitat features we considered in this study are likely to be proxies of ephemeral oceanic features, such as upwelling zones and fronts, which enhance local foraging conditions for seabirds (Schneider, 1990; Benazzouz *et al.*, 2014). Direct examination of habitat selection for such ephemeral features at a finer scale may yield more informative results.

Male kittiwakes foraged in shallower areas than females during incubation. Sex differences in habitat selection are common, and often ascribed to differences in morphology, breeding roles, or energetic requirements (Steffe *et al.*, 1989; Ardia *et al.*, 1997; Phillips *et al.*, 2004; Catry *et al.*, 2006; Pinet *et al.*, 2012). Competition may play a role in sexual segregation of foraging habitat (e.g. Marra 2000; Phillips *et al.* 2011), but given that we did not detect sex differences in habitat selection during chick rearing, when kittiwakes are constrained to forage within a smaller range, this explanation seems unlikely. Sex differences foraging habitat can also arise from differences in prey capture

techniques between the sexes: for example, Cleasby *et al.* (2015) suggested that the deeper diving behaviour of female gannets (*Morus bassanus*) may be advantageous in more stratified waters, where they foraged more frequently than males. Alternatively, while male and female kittiwakes share the role of incubation (Coulson, 2011), the costs of egg production for females may result in sex-specific nutritional requirements during incubation (Carey, 1996), which could lead to individual segregation in foraging habitat, as discussed previously in the context of boldness.

Despite predictions that animals should select habitat based upon their phenotype (Jacob *et al.*, 2015), we found high levels of individual variation in habitat preference were unexplained by personality or sex in kittiwakes. This is surprising, particularly during chick rearing, given the high levels of consistency individuals showed in habitat selection across two years, suggesting that kittiwakes do exhibit intrinsic differences in habitat preference. This raises the question of which factors do explain such variation. Other factors which influence individuals' foraging abilities, or energetic requirements, such as variation in age (Ficetola *et al.*, 2013; Lesmerises *et al.*, 2017), morphology (Baker, 1979; van de Pol *et al.*, 2010), or indeed other components of personality (see Toscano *et al.* 2016), may play a role. Further research into the individual determinants of habitat selection is required in order to understand the habitat requirements of animal populations, particularly in the context of marine predators, which are known to exhibit high levels of individual variation in foraging behaviour (Ceia *et al.*, 2015; Phillips *et al.*, 2017).

4.3 Individual consistency in habitat selection

We found striking differences in the repeatability of habitat selection between bold and shy kittiwakes during chick rearing: bold individuals exhibited high repeatability in their selection for all four environmental covariates, while shy individuals were not repeatable in their usage of bathymetry and glacier fronts. High repeatability may indicate that bold kittiwakes are more specialised than shy individuals in their habitat preferences. A growing body of evidence links boldness to high repeatability and individual consistency in behaviour, in particular with respect to foraging behaviour (Verbeek *et al.*, 1994; Marchetti *et al.*, 2000; Harris *et al.*, 2020). It is notable that shy individuals exhibited lower repeatability for two static habitat features – bathymetry

and glacier fronts – but not for the dynamic feature, SST. We predicted that bold individuals may select primarily for static habitat features, while shy individuals track dynamic cues of foraging habitat availability. Although we found no directional relationship between boldness and selection for SST, that shy kittiwakes were consistent in their usage of SST may indicate that individuals consistently track either high or low temperature cues; meanwhile, shy individuals may lack consistency in their usage of bathymetry and glacier fronts because they use these features variably, dependent upon the prevailing conditions when they leave the nest to forage.

Variable foraging behaviour among shy individuals may pertain from their general tendencies towards more flexible behaviour (Benus *et al.*, 1990; Verbeek *et al.*, 1994; Coppens *et al.*, 2010). Alternatively, shy individuals may be forced to forage more variably if they are outcompeted from the habitats used by bold individuals (Patrick *et al.*, 2014). Finally, differences in the repeatability of habitat selection may be linked to the patterns of boldness-dependent foraging site fidelity we previously reported in this population (Harris *et al.*, 2020). However, while we linked boldness to foraging site fidelity during incubation previously, here a link between boldness and repeatability of habitat selection was found only during the chick rearing phase. This implies that the two findings are not causally linked (i.e. patterns of foraging site fidelity are not an artefact of differences in habitat selection), but instead that similar mechanisms may generate relationships between boldness and individual consistency in kittiwake foraging behaviour.

5.0 Conclusions

Our study demonstrates profound individual differences in habitat selection in a wide-ranging marine predator, which are partly explained by individual characteristics of boldness and sex. Further, we report that shy individuals are less repeatable in their habitat selection, which may reflect a greater tendency for shy individuals to be foraging generalists. We find often opposing habitat preferences among individual kittiwakes, with some individuals consistently avoiding the habitat features selected for by other. This result corroborates the conclusion of two recent studies that accounting for

individual variability is crucial to avoid uninformative habitat selection estimates (Leclerc *et al.*, 2016; Lesmerises *et al.*, 2017). This is particularly relevant for conservation management efforts which aim to conserve species by targeting the population-level average foraging habitat (e.g. Chivers *et al.* 2013; Wakefield *et al.* 2017). Understanding the full extent of individual variability and its drivers is key to establishing effective conservation strategies for species experiencing rapid changes in habitat availability.

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Supplementary Materials to Chapter 3: Does personality predict individual habitat selection in a marine predator?

Appendix S3.A – Sex data

S3.A1 Sexing by DNA analysis

Of the 103 individuals used in the final analyses of the effects of boldness and sex on habitat selection, 98 were sexed by molecular analysis of DNA extracted from blood or feather samples. Sex was determined by DNA analysis following the protocol described in Chapter 2 (Appendix S2.A)

S3.A2 Sexing by morphometrics

Five individuals for which DNA samples were not obtained were assigned sex by morphometric assessment of head-bill length, following Jodice et al. (2000) and Coulson (2009). We performed a linear discriminant function analysis in the R package MASS (Venables & Ripley 2002) on headbill length to classify individuals as either male or female. This method was accurate for 90.7% of individuals for which sex was determined by genetic analysis.

S3.A3 No sex differences in boldness

We used a linear model with boldness as the response variable and sex as a fixed effect to test for sex differences in boldness. Males and females showed no difference in boldness ($F_{(1,101)} = 1.42$, $p = 0.24$; Figure S3.A1).

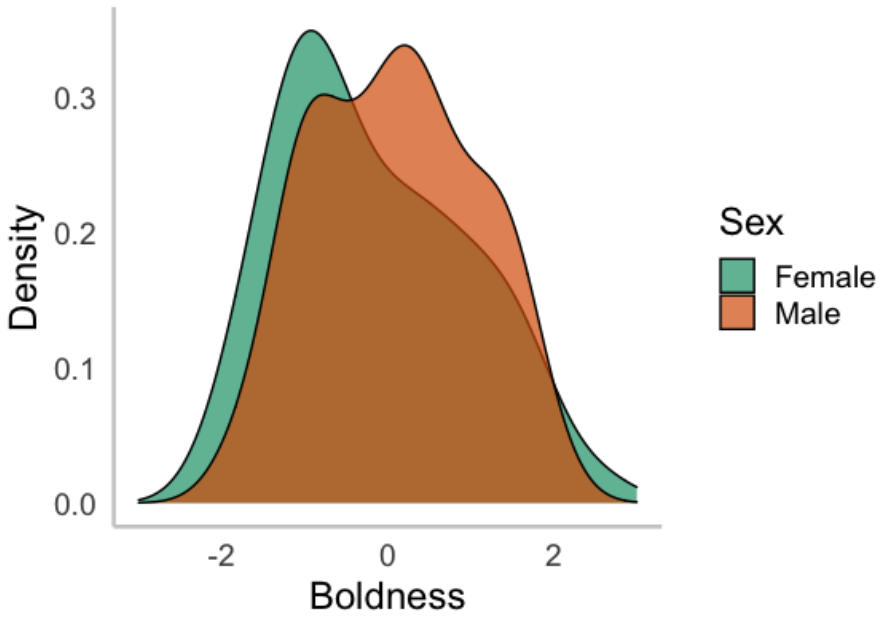

Figure S3.A1. Boldness did not significantly differ among males and females.

Appendix S3.B – Boldness test PCA

Table S3.B1. Variable loadings and cumulative variance explained for each Principal Component of the boldness test PCA.

Behaviour	PC1	PC2	PC3	PC4	PC5
Sitting	0.74	0.46	0.13	0.17	0.45
Raised up	0.01	-0.67	0.56	0.20	0.45
Standing	-0.05	-0.26	-0.79	0.32	0.45
Off the nest	-0.02	-0.04	-0.09	-0.89	0.45
Off the ledge	-0.67	0.52	0.20	0.19	0.45
Cumulative variance explained	0.57	0.83	0.96	1.00	1.00

Appendix S3.C – GPS logger types

S3.C1 Sample sizes for each logger type

Kittiwakes were equipped with one of three different GPS logger models: i-GotU GT-120, CatLog Gen 1, or CatLog Gen2. To reduce logger mass, a number of i-GotU and CatLog Gen1 loggers were modified to carry a smaller battery (lighter by 2.22-4.47g). The numbers of each type of logger deployed, and average mass of each logger type, are detailed in Table S3.C1.

Table S3.C1. Sample sizes and mean masses of different GPS logger models and battery combinations.

GPS logger model	Battery type	Average mass (g) ± SD	Number used
i-GotU GT-120	Original	17.75 ± 0.59	35
i-GotU GT-120	Modified	13.28 ± 0.63	167
CatLog Gen1	Original	15.10 ± 0.34	6
CatLog Gen1	Modified	12.88 ± 0.43	10
CatLog Gen2	Original	7.18 ± 0.44	46

S3.C2 Effects of logger mass on habitat selection

We tested whether differences in logger mass influenced habitat selection estimates using linear mixed effects models in lme4 (Bates *et al.* 2014). Habitat selection estimates for each environmental covariate (bathymetry, seabed slope, glacier fronts, SST) during each breeding stage (incubation, chick rearing) were fitted as response variables in separate models with logger mass as a fixed effect and individual ID as a random effect. We found no effect of logger mass on habitat selection estimates of trips from any model (Table S3.C2), indicating variation in logger mass within the range used here was unlikely to drive differences in habitat selection.

Table S3.C2. Results from linear mixed effects models testing the effects of variation in logger mass on habitat selection estimates.

Breeding stage	Environmental covariate	Test statistic	P-value
Incubation	Bathymetry	$X^2_{(1)} = 0.80$	0.37
	Seabed slope	$X^2_{(1)} = 0.24$	0.62
	Glacier fronts	$X^2_{(1)} = 0.03$	0.86
	SST	$X^2_{(1)} = 0.02$	0.89
Chick rearing	Bathymetry	$X^2_{(1)} = 1.11$	0.29
	Seabed slope	$X^2_{(1)} = 0.07$	0.80
	Glacier fronts	$X^2_{(1)} = 0.21$	0.65
	SST	$X^2_{(1)} = 0.88$	0.35

Appendix S3.D – Hidden Markov models

Starting parameters for hidden Markov models used for behavioural classification are presented in table S3.D1.

Table S3.D1. Starting parameters (SL: step length; TA: turning angle) for each HMM. Four HMMs were fitted in total, one per breeding stage (incubation; chick rearing) and one per fjord system (Isfjorden; Kongsfjorden).

	Incubation		Chick rearing	
Behaviour	Isfjorden	Kongsfjorden	Isfjorden	Kongsfjorden
Resting	SL: 0.10 ± 0.20 TA: μ = 0, κ = 25	SL: 0.01 ± 0.10 TA: μ = 0, κ = 25	SL: 0.07 ± 0.04 TA: μ = 0, κ = 25	SL: 0.04 ± 0.03 TA: μ = 0, κ = 25
Foraging	SL: 1.00 ± 1.00 TA: μ = pi, κ = 1	SL: 1.00 ± 1.00 TA: μ = 0, κ = 1	SL: 0.20 ± 0.26 TA: μ = pi, κ = 0.3	SL: 0.20 ± 0.26 TA: μ = pi, κ = 0.3
Commuting	SL: 5.00 ± 4.50 TA: μ = 0, κ = 13	SL: 3.00 ± 4.00 TA: μ = 0, κ = 13	SL: 1.20 ± 0.80 TA: μ = 0, κ = 14	SL: 1.00 ± 0.80 TA: μ = 0, κ = 14

Appendix S3.E – Selection of available habitat points for resource selection models

S3.E1 Colony- and year-specific foraging ranges

Resource selection functions were used to assess kittiwake habitat selection by comparison of environmental covariates at kittiwake foraging locations ("used" locations) with at randomly selected "available" locations. We selected available locations from within the maximum foraging ranges of kittiwakes, specific to year, colony, and breeding stage (reported in Table S3.E1).

Table S3.E1. Maximum foraging ranges (km) within each colony, year, and breeding stage. Available habitat points were randomly selected from within these ranges.

		Maximum foraging range (km)	
Colony	Year	Incubation	Chick rearing
Blomstrand	2017	511.76	46.64
Krykkjefjellet	2017	49.66	22.81
Observasjonholmen	2017	483.29	27.42
Observasjonholmen	2018	256.58	196.83
Grumantbyen	2017	525.42	306.66
Grumantbyen	2018	446.15	149.59
Pyramiden	2018	410.19	210.56

S3.E2 Selection of the ratio of available to used locations

Habitat selection estimates from resource selection functions are subject to variation dependent on the ratio of available locations to which used locations are compared. We determined the optimal ratio for our analyses following the methods of Trevail (2019). Briefly, we ran resource selection functions for bathymetry on our chick-rearing kittiwake dataset, with the ratio of available to used locations ranging from 1:1 and 10:1. Model structure matched that described in the main paper, with fixed effects for bathymetry (log transformed), distance to the colony (square root transformed), colony, and year, and a random slope and intercept at the trip level.

We compared selection estimates from these models at both the trip level (random slopes for each trip), and the population level (global slope estimates, representing bathymetry selection for all kittiwakes), in order to select the minimum ratio of available

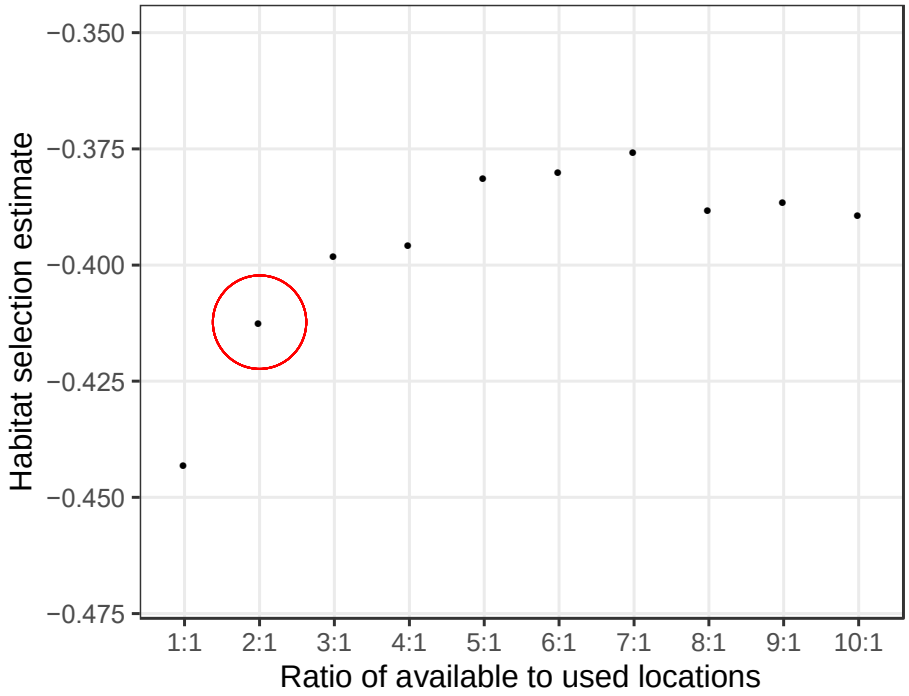

Figure S3.E1. Habitat selection estimates remained statistically constant above a ratio of 2:1 available to used locations.

locations yielding accurate selection estimates. At the trip level, we used a linear mixed effects model with selection estimate as the response variable, ratio as a fixed effect, and trip ID as a random effect, to test whether the number of available locations influenced selection estimates. At the population level, we visually determined the minimum number of available locations above which selection estimates did not change, validating this with a linear regression.

At the trip level, there was no effect of the ratio of available to used locations on trip selection estimates ($\chi^2_9 = 3.47$, $p = 0.94$). At the population level, we found no significant differences in selection estimates beyond a 2:1 ratio of available to used locations ($F_{1,3} = 4.05$, $p = 0.08$; Figure S3.E1).

Appendix S3.F – Environmental covariates

S3.F1 Validation of a 10km buffer to estimate SST data by bilinear interpolation

To yield accurate estimates of SST for locations where SST data could not be remotely sensed (N = 20,676, 11% of locations), we applied a spatial buffer within which we linearly interpolated SST values from surrounding grid cells. An initial buffer size of 1km was only sufficient to estimate SST for a further 166 locations (0.09%), so we further increased this buffer by stepwise increments of 1km up to a maximum of 10km. We validated a buffer size of up to 10km by randomly sampling 1,000 locations for which SST data were available with no buffer applied, and compared real SST values with SST estimated by application of a 10km buffer. Correspondence between real and estimated SST was very high ($R^2 = 0.97$, $p < 0.0001$, Figure S3.F1), supporting the use of a buffer of up to 10km to estimate SST.

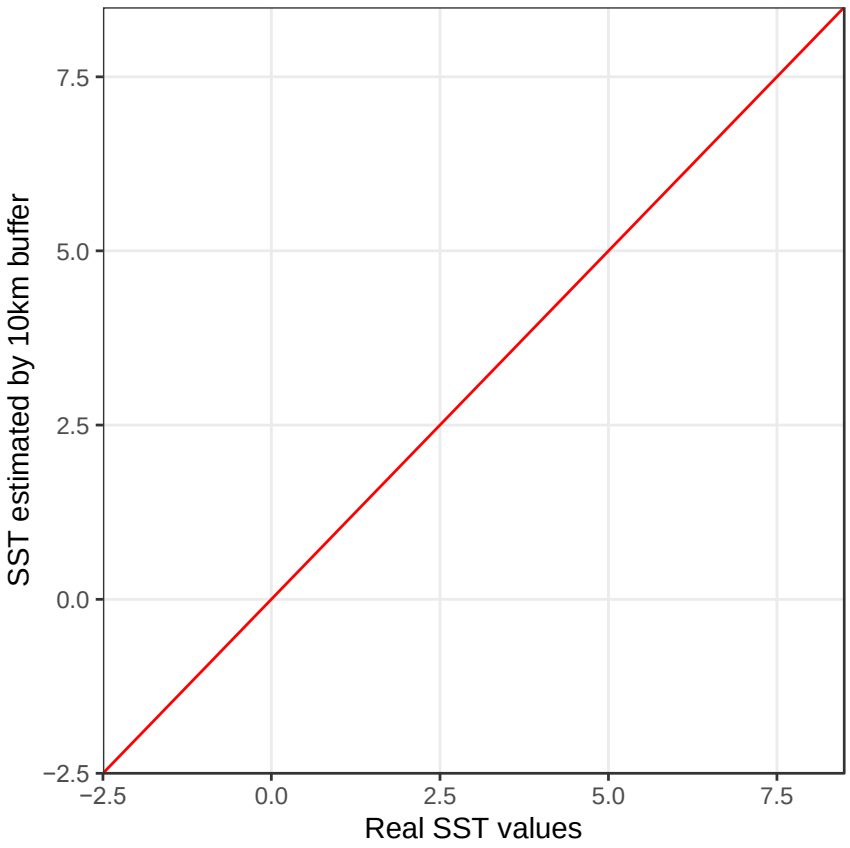

Figure S3.F1. SST values as estimated by fitting a 10km buffer around locations showed high correspondence to real SST values, based on 1,000 randomly selected locations for which SST was known. Points are plotted over the 1:1 line (red) as a visual aid.

S3.F2 Relationships among environmental covariates

We assessed correlations among pairs of environmental covariates using Spearman's rank correlation tests. Correlations are presented in Figure S3.F2 (figure produced using package PerformanceAnalytics (Peterson & Carl 2020).

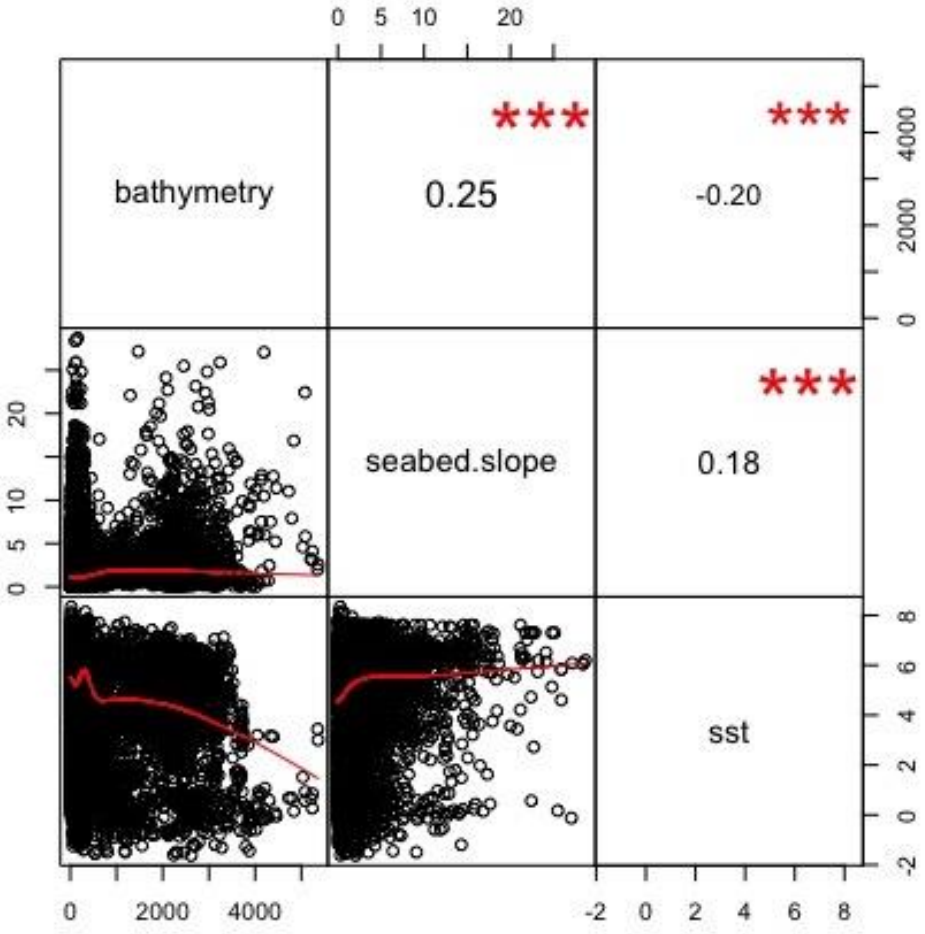

Figure S3.F2. Correlations among environmental covariates used in habitat selection models (bathymetry, seabed slope, SST). Upper right-hand panels contain correlation coefficients and significance levels ($p < 0.001$***; $p < 0.01$**; $p < 0.05$*) for Spearman's rank correlations tests among pairs of covariates. Lower left-hand panels contain bivariate scatterplots with fitted lines.

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Chapter 4

Personality-specific carry-over effects of winter foraging on breeding

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Personality-specific carry-over effects of winter foraging on breeding

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Abstract

Carry-over effects describe the phenomenon whereby an animal's previous conditions influence its subsequent performance. Carry-over effects are unlikely to impact individuals uniformly, but the factors modulating their strength are poorly known. Variation in the strength of carry-over effects may reflect individual differences in pace-of-life: slow-paced, shyly behaved individuals are thought to favour allocation to self-maintenance over current reproduction, compared to their fast-paced, boldly behaved conspecifics (the pace-of-life syndrome hypothesis). Therefore, detectable carry-over effects on breeding should be weaker in bolder individuals, as they should maintain allocation to reproduction irrespective of previous conditions, while shy individuals should experience stronger carry-over effects. We tested this prediction in black-legged kittiwakes breeding in Svalbard. Using miniature biologging devices, we measured non-breeding foraging activity of kittiwakes, and monitored their subsequent breeding performance to measure carry-over effects. We report negative carry-over effects of non-breeding activity, and found that carry-over effects on breeding were stronger in shyer individuals: active winters were followed by later breeding phenology and poorer breeding performance in shy birds, but these effects were weaker or undetected in bolder individuals. Our study quantifies individual variability in the strength of carry-over effects on breeding, and provides a mechanism explaining widespread differences in individual reproductive success.

Keywords: carry-over effects; boldness; life-history trade-offs; pace-of-life syndrome; reversible state effects; annual cycle; non-breeding season

1.0 Introduction

A fundamental challenge in ecology is understanding why individuals vary in breeding performance. An animal's previous history can be a major determinant of its fitness later in life, a phenomenon referred to as carry-over effects (Marra, 1998; Harrison *et al.*, 2011; O'Connor *et al.*, 2014; Senner *et al.*, 2015). In particular, events and processes that occur prior to the current breeding season (e.g. during the non-breeding season or in previous breeding seasons) can carry over to impact future breeding success (Harrison

et al., 2011). For example, studies have demonstrated that factors such as food availability (Robb *et al.*, 2008; Legagneux *et al.*, 2012), hormone levels (Harms *et al.*, 2014; Sanderson *et al.*, 2014), habitat use (Inger *et al.*, 2010; Sedinger *et al.*, 2011), and foraging behaviour (Shoji *et al.*, 2015; Clay *et al.*, 2018) outside the breeding season can all influence subsequent reproduction. Individuals can differ in how they respond to conditions (Nussey *et al.*, 2007), and therefore intrinsic variation is thought to be important (Daunt *et al.*, 2014). However, the sources of individual variation in carry-over effects remain poorly understood.

Carry-over effects result from life-history trade-offs among competing functions (O'Connor *et al.*, 2014; Varpe, 2017), but are rarely framed as such. When energetic reserves are limited, high allocation to current reproduction reduces potential allocation to somatic maintenance, future breeding, and survival, and so animals may divert resources away from current breeding towards other functions (Williams, 1966; Stearns, 1989, 1992). Examining carry-over effects in the framework of life-history trade-offs may offer new insights into the intrinsic factors which shape them. This is because the trade-off between current versus future reproduction also manifests in the form of different life-history strategies at the individual level. Life-history strategies are thought to occur along a fast-slow pace-of-life continuum, whereby a fast pace-of-life is characterised by high allocation to current breeding and low survival (Stearns, 1989; Ricklefs *et al.*, 2002; Jones *et al.*, 2008). It may then be predicted that individual differences in pace-of-life should be reflected in the strength of carry-over effects on current breeding, with stronger effects of previous conditions on breeding in slow-paced than in fast-paced animals.

At the among-individual level, variation in pace-of-life is thought to be linked to phenotypic differences in behavioural traits, or animal personalities (the pace-of-life syndrome hypothesis; Réale *et al.*, 2010). Individuals adopting a slow pace-of-life should minimise risk-taking behaviours to favour survival probability, while fast-paced individuals should adopt risky (or "bold") behaviours that facilitate current reproduction (Stamps, 2007; Réale *et al.*, 2010). Boldness should therefore predict variation in carry-over effects. While challenging winter conditions should result in reduced allocation to breeding in shy, slow-paced animals, boldly behaved, fast-paced

individuals should maintain allocation to reproduction, such that carry-over effects are weaker or undetected.

Here, we investigate personality as a predictor of carry-over effects on breeding in a species of seabird, the black-legged kittiwake (*Rissa tridactyla*). A previous study has demonstrated that pace-of-life can shape allocation trade-offs in two kittiwake populations differing markedly in pace-of-life. Following experimentally-induced stress, birds from the fast-paced population maintained provisioning rates and successfully reared offspring, whereas slow-paced individuals reduced parental care, resulting in decreased offspring survival (Schultner *et al.*, 2013). Populations of the same species are often shown to vary in pace-of-life, likely driven by their evolution under different ecological conditions (Wikelski *et al.*, 2003). By contrast, empirical examination of the pace-of-life syndrome at the individual level has yielded mixed results, despite theoretical support for its existence (Wolf *et al.*, 2007; Réale *et al.*, 2010). An increasing body of evidence demonstrates that individual variation in allocation trade-offs is highly prevalent in the form of naturally occurring carry-over effects between seasons, with profound consequences for individual fitness (Harrison *et al.*, 2011). However, to our knowledge, no study has previously tested whether differences in carry-over effects can be explained by individual variation in pace-of-life.

While sources of variation in carry-over effects are poorly known, sex-dependent carry-over effects have been reported in a number of systems (Sorensen *et al.*, 2009; Drake *et al.*, 2013; Pérez *et al.*, 2016; Saino *et al.*, 2017). Sex-dependent carry-over effects can arise due to sex differences in breeding roles. For instance, a number of studies on birds have reported that carry-over effects on breeding phenology are stronger in females than in males, potentially due to greater control over the timing of egg laying by females (Ball *et al.*, 2008; Sorensen *et al.*, 2009; Drake *et al.*, 2013; Saino *et al.*, 2017). Sex differences in pace-of-life may also generate variation in carry-over effects: owing fundamentally to gamete dimorphism (anisogamy), males are generally expected to exhibit a faster pace-of-life relative to females, allocating towards reproductive output over longevity (Vinogradov, 1998; Bonduriansky *et al.*, 2008; Maklakov *et al.*, 2013; Hämäläinen *et al.*, 2018). As a result, females may be subject to stronger carry-over effects on breeding,

even in species where the sexes do not differ greatly in breeding roles (e.g. Saino *et al.*, 2017). We therefore also examined sex differences in carry-over effects.

We examined carry-over effects on breeding using a long-term biologging dataset on kittiwakes breeding in Svalbard. Kittiwakes breeding in Svalbard migrate to the west Atlantic for the winter, which they spend at sea (Frederiksen *et al.*, 2012). High levels of foraging activity during the non-breeding season have been shown to negatively affect subsequent breeding performance in a number of seabird species (Daunt *et al.*, 2014; Shoji *et al.*, 2015; Clay *et al.*, 2018). We quantified kittiwakes' activity during the non-breeding season and linked this to spring migration phenology (date of arrival back to the colony), breeding phenology (lay date), and breeding performance (offspring survival) in order to measure carry-over effects. We then tested for interactions between personality and carry-over effects, to test the prediction that carry-over effects reflect differences in pace-of-life. Our predictions were that non-breeding activity will have negative carry-over effects on the subsequent breeding season, such that high activity will be associated with later phenology and reduced breeding performance, and that these negative carry-over effects will be stronger in shy than in bold individuals. As kittiwakes are sexually monomorphic and exhibit biparental care (Coulson, 2011), we did not expect strong differences between the sexes, but expected that in line with other studies, carry-over effects on the timing of breeding may be stronger in females due to greater control over the timing of egg laying.

2.0 Materials and Methods

2.1 Study system

Black-legged kittiwakes lay 1-3 eggs (but usually two) and exhibit biparental care throughout the breeding season. We studied kittiwakes nesting on an empty building in the abandoned mining town of Grumantbyen (78°10'N 15°05'E), in Isfjorden on the west coast of Svalbard. Kittiwakes have been ringed and monitored during the breeding season at this site since 2008. Approximately 40 pairs breed at Grumantbyen each year. Nests were monitored from laying in early June to late chick rearing in late July. Early in the season, nests were checked weekly using a mirror mounted on the end of a pole to

record number of eggs until probable hatching time began, at which point nests were checked every 2-3 days to record number and presence of eggs and chicks. Records from nest monitoring were used to obtain birds' lay date and breeding performance each year. Lay date was defined as the first day on which a bird's nest contained an egg (days since January 1st of that year). In some years we observed extremely low fledging success at the colony. To assess variation in birds' abilities to rear offspring, we therefore used the number of days survived by birds' offspring from the lay date as the measure of breeding performance. Molecular sexing of breeding kittiwakes was conducted on DNA extracted from blood and feather samples following the methods described in Appendix S3.A.

2.2 Boldness tests

In 2017 and 2018, we measured boldness of adult breeding kittiwakes using a novel object test, following an existing protocol (Harris *et al.*, 2020). Briefly, we measured individuals' response to a blue plastic penguin toy presented at the nest for 60 seconds, recording the proportion of the test an individual spent in each of five mutually exclusive behavioural states: (1) sitting on the nest; (2) body raised off nest cup, but not standing; (3) standing on the nest (legs visible and extending to the base of the nest); (4) off the nest but remaining on the cliff or window ledge close to the nest; (5) off the cliff or window ledge (and no longer visible). Over two years, 80 individuals were tested: 36 individuals were tested once, 20 were tested twice, 15 were tested three times, and 9 were tested more than three times. 27 individuals were tested in both 2017 and in 2018. Using a Principal Component Analysis (PCA), we collapsed the five behavioural variables into a single test score (PC1; see Appendix S4.A for variable loadings). This score has been shown to be highly repeatable in kittiwakes within a single breeding season ($R = 0.68$; CI: 0.57-0.79; $p < 0.001$; Harris *et al.*, 2020). We measured adjusted repeatability of PC1 (repeatability after controlling for confounding effects; Nakagawa *et al.*, 2010) across two breeding seasons using the R package *rptR* (Stoffel *et al.*, 2017), including fixed effects to adjust for test date, breeding stage (incubation or chick rearing), and test number (the number of times an individual had previously been tested). Finally, following Quinn *et al.* (2009), we extracted a single estimate of boldness per individual using a linear model with PC1 fitted as the response variable, and individual ID, test date, breeding stage, and test number fitted as fixed effects. We find no difference in boldness between the sexes (results from a linear model comparing boldness by sex: $p = 0.19$).

2.3 Non-breeding activity

Between June 2012 and August 2018, adult kittiwakes were equipped with geolocator-immersion loggers of either the MK4083 series (Biotrack, 17 x 10 x 6.5mm, 1.9g) or C65 series (Migratetech, 14 x 8 x 6 mm, 1.0g), attached to plastic leg rings. The loggers record patterns of immersion in saltwater, enabling inference of behavioural patterns in marine species. Immersion loggers were deployed with the aim of retrieval after one year to obtain data on the non-breeding period, but in some cases were retrieved after more than one year where birds were not captured during a given season (loggers retrieved after one year: N = 71; loggers retrieved after two years: N = 4). After logger retrieval, most individuals were re-equipped with a new logger to record activity during the following non-breeding season. MK4083 loggers tested for saltwater immersion every 3 seconds, and C65 every 30 seconds, both storing the sum of "wet" readings within a 10-min bout. To facilitate comparison between logger types, we divided the values derived from MK4083 loggers by 10 such that data from both logger types ranged from 0 (continuously dry for 10-min) to 20 (continuously wet for 10-min).

Kittiwakes rest on the sea surface during the winter months, and only spend significant time on land during the breeding season, when attending their nests (Daunt *et al.*, 2002; Frederiksen *et al.*, 2012). Kittiwakes are surface feeders, foraging from the surface of the water or by shallow dives from the air (Burger, 1988; McKnight *et al.*, 2011). As per McKnight *et al.* (2011), we defined 10-min periods spent entirely dry as bouts of flight, and 10-min periods with at least 95% wet readings as bouts of resting on the sea. 10-min periods with 5-95% wet readings were defined as bouts of probable foraging behaviour, except for in cases where a single 10-min period of intermittent wet readings occurred in between a period of flight and rest, as these are likely to indicate the transition between flying and resting behaviours (McKnight *et al.*, 2011). We identified the start and end of the non-breeding period for each bird using the percentage of daily time spent resting on the sea. The first day of the year on which a bird spent no time resting on the sea was regarded as its first day spent at the colony (colony arrival date), and the last day with no time spent resting on the sea as its last day at the colony (colony departure date). Each individual's non-breeding season was then defined as the interval between colony departure and arrival dates. We then extracted the daily proportion of time spent foraging, in flight, and resting, for each day of the non-breeding season. Time

spent in flight and time spent resting were strongly negatively correlated ($R = -0.88$, $p < 0.001$) while there was a weak negative correlation between time in flight and time spent foraging ($R = -0.22$, $p < 0.001$). As indicators of non-breeding activity, we averaged the daily proportion of time spent (i) foraging and (ii) in flight across all days of the non-breeding season. As kittiwakes locate prey during flight (Coulson, 2011), both time in flight and time spent foraging are likely to represent birds' foraging effort. We recorded non-breeding activity data over 78 bird-years in total, for 39 boldness-tested individuals over 6 years of study (22 males in 41 bird-years, and 17 females in 37 bird-years), with a mean of two bird-years per individual (range 1-5 years).

2.4 Statistical analysis

Analyses were conducted in R version 3.5.1 (R Core Team, 2018) using the *lme4* package (Bates *et al.*, 2015) for fitting LMMs. Prior to testing for carry-over effects on breeding, we first determined whether kittiwakes varied in their non-breeding activity with boldness and sex. We fitted time spent in flight and time spent foraging as response variables in two separate linear mixed effects models (LMMs), with boldness, sex, and their two-way interaction fitted as fixed effects, and bird identity and year fitted as random effects. Model selection was conducted using an information-theoretic approach, using Akaike's Information Criterion corrected for small sample sizes (AIC_C). We built a candidate set of models from all possible combinations of predictors, and refined these to a top model set by ranking according to AIC_C, selecting the model structure that minimised AIC_C as the best model, and those within two AIC_C units as competitive (Burnham *et al.*, 2004). Because AIC can favour overly complex models (Burnham *et al.*, 2004), inference can be improved by eliminating models from the top model set if they are more complex versions of simpler (nested) models with lower AIC_C values, known as the "nesting rule" (Arnold, 2010; Richards *et al.*, 2011; Harrison *et al.*, 2018). We therefore applied the nesting rule to prevent the retention of overly complex models. When multiple models remained in the top set after applying the nesting rule, we made inference of the importance of predictors based on model-averaged parameter estimates (Arnold, 2010).

To examine how non-breeding activity may carry-over to influence subsequent breeding, we considered effects on colony arrival date, lay date, and breeding

performance. Colony arrival date (days since January 1st of that year) was defined as the first day a bird spent back at the breeding colony, as identified by immersion loggers. In separate LMMs with Gaussian distributions, we fitted colony arrival date, lay date and offspring survival as response variables, and included the following predictors: (i) time in flight, (ii) time foraging, (iii) boldness, and the two way interactions between (iv) time in flight and boldness and (v) time foraging and boldness. Because date of arrival to the breeding colony can influence timing of breeding, and both the timing of arrival and of breeding can influence breeding success (Harms *et al.*, 2014), we additionally included (vi) colony arrival date as a fixed effect in lay date and offspring survival models, and (vii) lay date in offspring survival models. Colony arrival date and lay date were weakly correlated (supplementary material Appendix S4.B), but for all models we inspected variance inflation factors (Zuur *et al.*, 2009) of predictor variables and found no evidence of collinearity (<2.5 in all cases). Bird identity and year were fitted as random effects. We ran all carry-over effects models separately for males and females to control for non-independence of breeding outcomes between paired birds. Model selection was conducted using AIC_C, as specified above. We calculated conditional R^2 (variance explained by both fixed and random effects) for all top-ranking models using the *MuMIn* package (Barton, 2018). All variables were standardised (to a mean of 0 and standard deviation of 1) to facilitate model fitting. Boldness was square-root transformed to approach a normal distribution.

3.0 Results

3.1 Boldness

PC1 explained 58.51% of the variation in response to the novel object, and across two years individuals were highly repeatable in their test responses (R = 0.61, CI: 0.48-0.73; p < 0.001). Boldness scores ranged from -0.86 to 1.36 with low values representing "shy" responses and high values representing "bold" responses. These results are comparable with findings from a single year of personality testing on black-legged kittiwakes (Harris *et al.*, 2020).

3.2 Variation in non-breeding season activity

We did not find an effect of boldness, sex, or their two-way interaction on kittiwake non-breeding activity: after applying the nesting rule, the best supported models predicting variation in both time spent foraging and time in flight during the non-breeding season containing only model intercepts (see Table S4.C1 in the Appendix for full model results).

Table 4.1. Summaries of best supported models of carry-over effects of non-breeding activity on colony arrival date, lay date, and offspring survival. Estimates are presented for predictors retained in best supported models only, which were those retained when ΔAICc < 2 and where there was no simpler outranking model (the "nesting rule", Arnold 2010). Conditional R^2 is reported for all models. Models were run separately by sex (M: males; F: females). Bird ID and season were fitted as random effects in all models. Arrival date and lay date were controlled for in offspring survival models, and arrival date was controlled for in lay date models (these variables are in grey for their own respective models where they were not fitted as fixed effects). Full model tables are presented in Appendix S4.D.

Response	Sex	Inter-cept	Bold.	Foraging	Flight	Bold. x foraging	Bold. x flight	Arrival date	Lay date	ΔAICc	R^2
Arrival date	M	118.00	0.28	2.40	0.01	-2.15	-2.06			0.00	0.72
		118.80	-	1.82	-	-	-			0.13	0.52
	F	119.20	1.97	-	2.48	-	-			0.00	0.59
Lay date	M	162.94	-	2.21	1.40	-	-	-		0.00	0.27
		162.96	-	1.54	-	-	-	-		1.13	0.26
	F	161.63	2.76	-	2.96	-	-1.77			0.00	0.61
Offspring survival	M	13.12	-0.34	-2.06	-	2.23	-	-	-1.35	0.00	0.48
		12.94	-0.39	-2.43	-	2.01	-	-	-	0.25	0.48
		13.08	-	-1.42	1.27	-	-	-	-1.23	1.00	0.47
		12.92	-	-1.89	1.00	-	-	-	-	1.27	0.46
		13.02	-	-2.09	-	-	-	-	-0.95	1.34	0.44
		12.90	-	-2.35	-	-	-	-	-	1.45	0.45
		13.12	-	-	2.00	-	-	-	-1.74	1.55	0.45
	F	14.41	-1.63	1.46	-	-	-	-	-	0.00	0.66
		14.57	-1.48	-	-	-	-	-	-1.15	0.36	0.60
		14.46	-2.11	-	-1.02	-	-	-	-	0.49	0.64
		14.40	-1.83	-	-	-	-	-	-	0.49	0.63
		14.65	-	1.36	-	-	-	-	-1.27	0.68	0.66
		14.49	-	1.73	-	-	-	-	-	0.85	0.70
		14.69	-	-	-	-	-	-	-1.71	0.95	0.59
		14.55	-	-	-	-	-	-1.10	-	1.83	0.60

3.3 Boldness and carry-over effects on breeding

Boldness was retained in the best-supported models of colony arrival date for females, as well as in one of two best-supported models for males, and for both sexes positive estimates indicated that bolder kittiwakes returned later to the breeding colony in spring (Tables 4.1-4.2; Figure 4.1). In females, but not males, boldness was associated with later egg laying (Tables 4.1-4.2; Figure 4.2). Boldness was also retained in a number of the best-supported models of offspring survival for males and females, indicating that bolder kittiwakes had lower offspring survival than shyer individuals (Tables 4.1-4.2; Figure 4.3). Later egg laying was also negatively associated with offspring survival (Tables 4.1-4.2).

Table 4.2. Model averaged estimated from the best supported models investigating the effects of winter activity and boldness on the subsequent breeding season. Best supported models were those retained in best supported models only, which were those retained when ΔAICc < 2 and where there was no simpler outranking model (the "nesting rule", Arnold 2010). Model averaged estimates ± standard errors are reported for predictors retained in best supported models only. Importance is the relative variable importance, calculated as the sum of Akaike weights of the models in which that term appears. Bird ID and season were fitted as random effects in all models. Arrival date and lay date were controlled for in offspring survival models, and arrival date was controlled for in lay date models (these variables are in grey for their own respective models where they were not fitted as fixed effects).

		Colony arrival date		Lay date		Offspring survival	
	Predictor	Est ± SE	Importance	Est ± SE	Importance	Est ± SE	Importance
Males	Intercept	118.41±2.30	-	162.94±1.33	-	13.02±2.95	-
	Boldness	0.28±0.99	0.52		0.00	-0.36±1.23	0.42
	Foraging	2.12±0.95	1.00	1.97±0.95	1.00	-2.06±1.32	0.90
	Flight	0.00±1.04	0.52	1.40±0.95	1.00	1.39±1.44	0.36
	Bold. x foraging	-2.15±1.03	0.52		0.00	2.13±1.32	0.42
	Bold. x flight	-2.06±1.10	0.52		0.00		0.00
	Arrival date				0.00		0.00
	Lay date					-1.31 ± 1.41	0.58
Females	Intercept	119.16±1.33	-	161.63±1.33	-	14.52±3.62	-
	Boldness	1.97±0.94	1.00	2.76±0.63	1.00	-1.75±1.37	0.59
	Foraging		0.00		0.00	1.50±1.32	0.41
	Flight	2.48±0.88	1.00	2.96±0.79	1.00	-1.02±1.50	0.14
	Bold. x foraging		0.00		0.00		0.00
	Bold. x flight		0.00	-1.77±0.62	1.00		0.00
	Arrival date				0.00	-1.10±1.52	0.07
	Lay date					-1.35±1.50	0.37

As we predicted, we detected predominantly negative effects of winter activity on breeding, but some positive effects. Among males, winters characterised by more time spent foraging were followed by later arrival to the colony, later egg laying, and lower offspring survival in the subsequent season (Tables 4.1-4.2; Figures 4.1-4.3), while more time spent in flight during the winter also predicted later egg laying (Tables 4.1-4.2; Figure 4.2). We also found a positive carry-over effect of non-breeding flight activity on offspring survival in males (Tables 4.1-4.2; Figure 4.3). Among females, more time spent in flight during the non-breeding season predicted later colony arrival, later egg laying and in one model, lower offspring survival, while more time spent foraging had positive effects on offspring survival (Tables 4.1-4.2; Figures 4.1-4.3).

We found evidence that carry-over effects on breeding were strongest for shy individuals: among males, more time spent foraging and in flight predicted later arrival to the colony particularly in shyer individuals (Table 4.1; Figure 4.1a; Figure 4.1c), and the negative effect of foraging activity on offspring survival was also stronger in shy than in bold males (Table 4.1; Figure 4.3c). Among females, an interaction between non-breeding activity variables and boldness was only supported in lay date models, where more flight activity predicted later egg laying most strongly in shy individuals (Tables 4.1-4.2; Figure 4.2b).

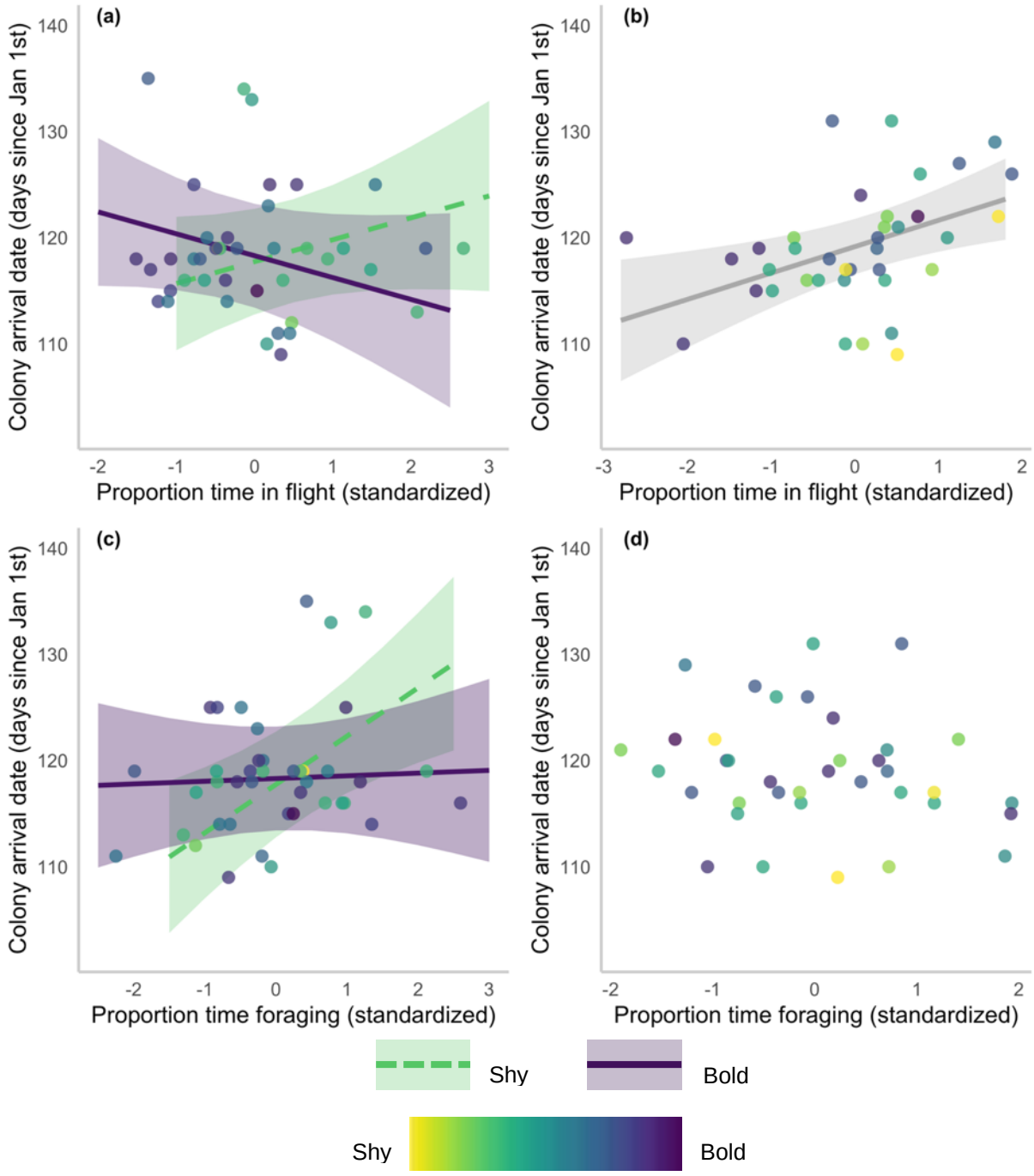

Figure 4.1. Carry-over effects of non-breeding activity (time spent in flight and time spent foraging) on colony arrival date for male (left) and female (right) kittiwakes. Point colour represents boldness from boldest (darkest) to shyest (lightest). Boldness is a continuous measure in all analyses, but where an interaction between boldness and activity was supported estimates are presented for the boldest individuals (+1 standard deviation from the mean) in darker solid lines, and for the shyest individuals (-1 standard deviation from the mean) in paler dashed lines. A single line indicates no interaction between activity and boldness, and no line indicates no effect of activity on arrival date. Shaded area represents 95% confidence intervals.

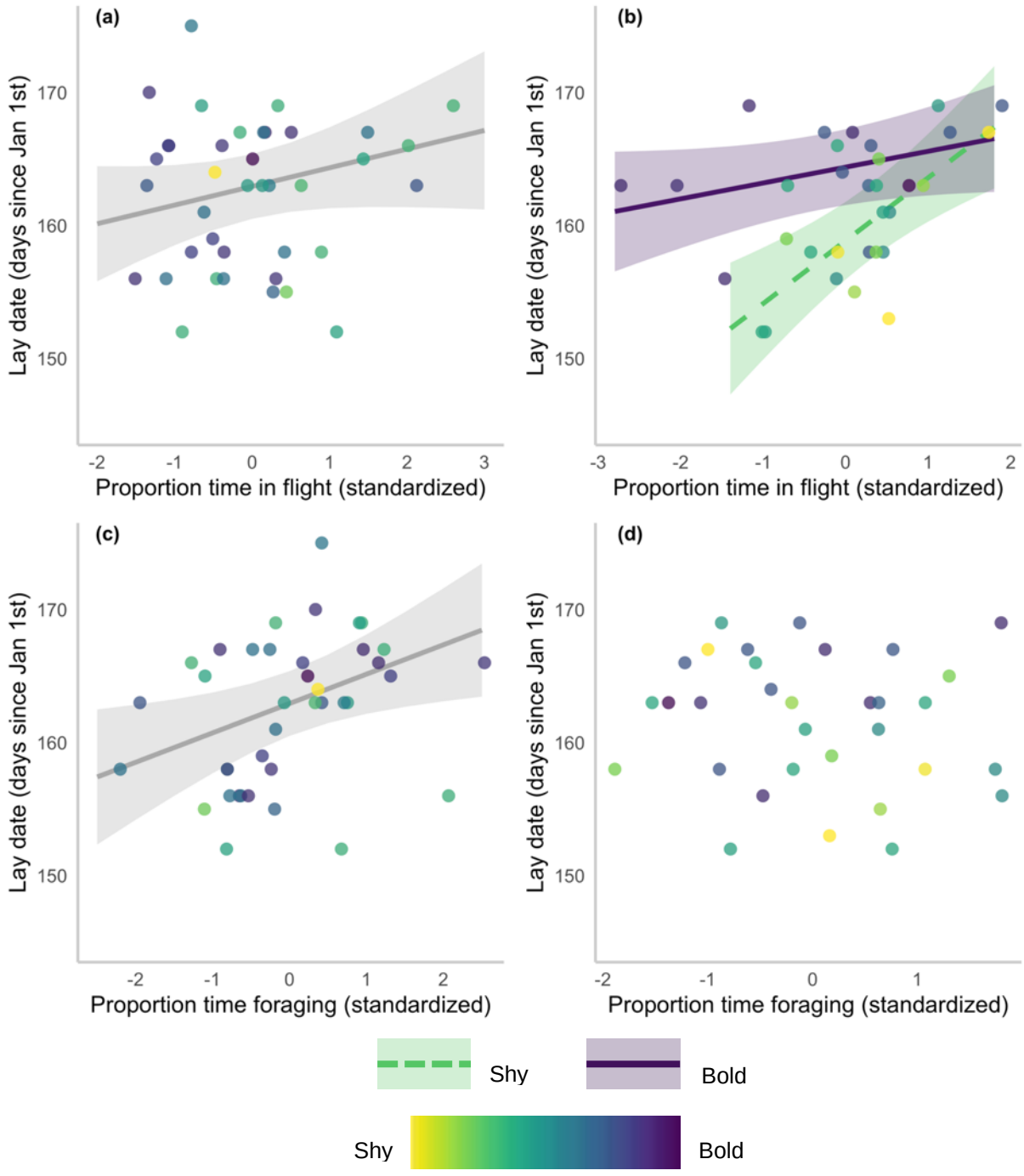

Figure 4.2. Carry-over effects of non-breeding activity (time spent in flight and time spent foraging) on lay date for male (left) and female (right) kittiwakes. Point colour represents boldness from boldest (darkest) to shyest (lightest). Boldness is a continuous measure in all analyses, but where an interaction between boldness and activity was supported estimates are presented for the boldest individuals (+1 standard deviation from the mean) in darker solid lines, and for the shyest individuals (-1 standard deviation from the mean) in paler dashed lines. A single line indicates no interaction between activity and boldness, and no line indicates no effect of activity on lay date. Shaded area represents 95% confidence intervals.

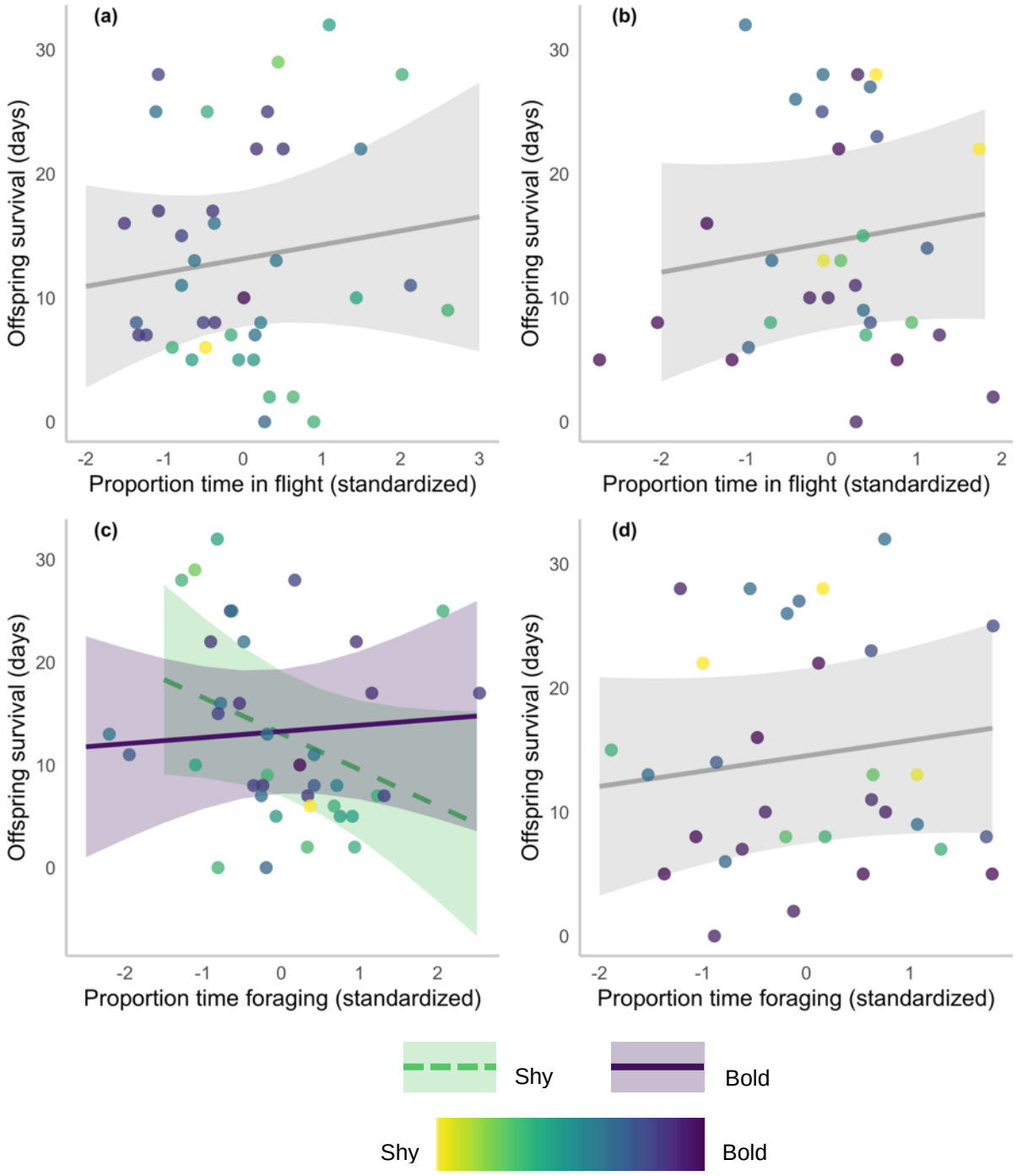

Figure 4.3. Carry-over effects of non-breeding activity (time spent in flight and time spent foraging) on offspring survival for male (left) and female (right) kittiwakes. Point colour represents boldness from boldest (darkest) to shyest (lightest). Boldness is a continuous measure in all analyses, but where an interaction between boldness and activity was supported estimates are presented for the boldest individuals (+1 standard deviation from the mean) in darker solid lines, and for the shyest individuals (-1 standard deviation from the mean) in paler dashed lines. A single line indicates no interaction between activity and boldness, and no line indicates no effect of activity on offspring survival. Shaded area represents 95% confidence intervals.

4.0 Discussion

Carry-over effects link individuals' activity during one season to their performance in subsequent seasons, but despite being measured at the individual level, examination of the factors shaping individual differences in carry-over effects has been lacking. This study is the first to investigate how carry-over effects are influenced by personality, and to demonstrate personality-specific carry-over effects. We find sex- and personality-dependent carry-over effects of non-breeding activity in kittiwakes. Males that foraged more actively during the non-breeding season arrived back later to the colony the following spring, began breeding later, and had lower offspring survival. For female kittiwakes, more time spent in flight was associated with later colony arrival, later egg laying, and lower offspring survival, while time spent foraging had a positive effect on offspring survival. Interactions between boldness and non-breeding activity supported personality-dependent carry-over effects, and in all supported interactions, we found that negative carry-over effects were stronger in shy individuals than in bolder individuals. These results provide support for the pace-of-life syndrome hypothesis that personality should be linked to life-history, and emphasise the importance of considering interactions with intrinsic factors when determining the consequences of carry-over effects for population dynamics.

4.1 Carry-over effects of non-breeding activity

There is increasing evidence that activity during the non-breeding season influences subsequent breeding performance (Daunt *et al.*, 2014; Shoji *et al.*, 2015; Clay *et al.*, 2018; Desprez *et al.*, 2018), facilitated by advances in biologging technology. In concordance with a number of other studies on seabirds (Daunt *et al.*, 2014; Shoji *et al.*, 2015; Clay *et al.*, 2018), we detected predominantly negative carry-over effects of time spent both flying and foraging on subsequent breeding performance in kittiwakes. Among males, spending more time foraging during the winter preceded later arrival back to the colony, later started clutches, and lower offspring survival; more time spent in flight was also associated with later laid eggs and lower offspring survival in males. Among females too, winters characterised by more time in flight preceded later return to the colony, later egg laying, and lower offspring survival. This suggests, in accordance with previous work (Daunt *et al.*, 2014; Shoji *et al.*, 2015; Clay *et al.*, 2018), that seabirds increase activity during the winter to compensate for poor foraging conditions, or for their own poor body

condition, such that more time and effort is required to acquire their daily food requirements (Shoji *et al.*, 2015). Individuals in poor condition may be forced to prolong their time at wintering grounds in order to attain condition sufficient for breeding (Bogdanova *et al.*, 2017), resulting in later return to the breeding grounds and later onset of breeding, and, if sufficient condition is not reached, reduced breeding success (Bêty *et al.*, 2003; Harrison *et al.*, 2013). Further, numerous studies have linked both poor winter body condition to reduced probability of attempting to breed at all the following season (Weimerskirch, 1992; Bêty *et al.*, 2003; Inger *et al.*, 2010). Due to insufficient data on individuals that did not attempt breeding in a given year, we were unable to test whether the effects of non-breeding activity carried over to influence breeding probability, but it may be predicted that such effects occur and have important consequences for population dynamics during years following poor wintering conditions.

4.2 Personality-dependent carry-over effects

A number of negative carry-over effects were stronger in shyer individuals than in bolder birds. Winters characterised by high activity were followed by later return to the colony and lower offspring survival in shy males, and later egg laying in shy females, but these effects were attenuated in bolder individuals, suggesting that variation in boldness is associated with differential breeding responses to non-breeding conditions. The directionality of these findings is consistent with the pace-of-life syndrome hypothesis, which predicts a coupling between life-history and personality, such that a fast pace-of-life should be associated with boldness and a slow pace-of-life with shyness (Réale *et al.*, 2010). Under challenging conditions, the trade-off between allocation to self-maintenance and to current reproductive effort is exacerbated (Zera *et al.*, 2001), forcing individuals to make decisions between allocating to one over the other. Our findings suggest that shy individuals may be more likely to respond to poor condition by allocating away from reproductive activities and instead towards self-maintenance. This may be achieved by spending longer at the wintering grounds (Bogdanova *et al.*, 2017), in order to spend more time foraging in order to regain lost condition, with detrimental effects on the timing of breeding and on breeding performance. In more extreme cases, where conditions are particularly poor, shy individuals may also be more likely to skip breeding for a year altogether, although we were unable to test this prediction owing to a lack of data on birds that skipped breeding. Bold individuals' breeding performance

and phenology was less dependent upon non-breeding activity, suggesting that bold individuals' breeding strategies involve high allocation to breeding attempts, irrespective of costs to an individual's condition. Interestingly, following what we interpret as "good" non-breeding conditions (when birds spent less time foraging and in flight), shy individuals performed equal to or even better than bold individuals. For example, shy males arrived earlier to the colony and had higher offspring survival following winters when they spent less time foraging and in flight. This suggests that bold and shy birds did not differ in quality, but in how they respond to non-breeding conditions.

The pace-of-life syndrome hypothesis has mixed support, with a recent meta-analysis demonstrating that evidence for correlations between individual behaviour and life-history is weak, particularly in vertebrate species (Royauté *et al.*, 2018). However, a recent review highlighted that a lack of support for the pace-of-life syndrome hypothesis may be due to phenotypic plasticity in response to the environment obscuring a clear link between personality traits and reproductive output (Campos-Candela *et al.*, 2019). Testing for a relationship between personality and breeding performance contingent on an individual's condition may remove confounding effects of environmental variation on breeding. A strong relationship between boldness and lifetime reproductive success, especially in species with restricted breeding opportunities, would likely lead to strong, directional selection and elimination of variation in boldness. Alternatively, an effect of personality on condition-dependent reproductive performance, as reported here, may result from behavioural life-history syndromes and evade directional selection.

Another way in which carry-over effects may interact with boldness is that carry-over effects could act upon personality traits themselves. Personality traits are typically characterised by their stability, but recent work has recognised the importance of within-individual changes in personality in response to environmental conditions, known as behavioural plasticity (Dingemanse *et al.*, 2010; Mathot *et al.*, 2015). Our method of assaying boldness captures individuals' propensity to defend their nest, and we might therefore expect that when carry-over effects of winter conditions lead an individual to invest less in reproductive performance, they should also behave more shyly. By assaying boldness in individuals over periods of several more years, it would

be possible to quantify individuals' plasticity in personality in relation to non-breeding conditions, and test whether carry-over effects also act upon personality traits. Furthermore, using longitudinal boldness data, future work could test whether individuals consistently differ in their plasticity in response to winter conditions (Biro *et al.*, 2010; Dingemanse *et al.*, 2010), and examine whether plasticity in personality is adaptive, and its consequences for lifetime fitness.

4.3 Sex-specific carry-over effects

Contrary to our prediction, lay date was driven not only by the non-breeding activity of females, but also that of males. A number of studies have reported that carry-over effects on the timing of egg laying are stronger in females than in males (Ball *et al.*, 2008; Sorensen *et al.*, 2009; Drake *et al.*, 2013; Saino *et al.*, 2017), attributing this to female control over the timing of egg laying (Caro *et al.*, 2009). Despite that females have direct control over when to lay, males in better body condition may advance their partner's lay date through earlier engagement in breeding behaviours such as nest building, courtship feeding and, ultimately, copulation (Goutte *et al.*, 2010). We suggest that males' activity during the non-breeding season has the potential to influence the timing of breeding through changes in condition required to initiate breeding behaviours.

Male and female kittiwakes showed differences in the non-breeding behaviours that influenced their subsequent breeding phenology and performance. For males, the strongest carry-over effects were of time spent foraging, while among females, time spent in flight affected phenology, but foraging did not. Furthermore, more time spent in flight preceded later breeding, but higher offspring survival in males, while in females, more time spent foraging improved offspring survival. These positive carry-over effects are firstly interesting in their own right: in all cases where we detected effects of non-breeding activity on phenology, effects were negative, which supported our interpretation that birds compensate for poor conditions by increasing foraging effort (Daunt *et al.*, 2014; Shoji *et al.*, 2015). One potential explanation for where these same non-breeding behaviours positively affected offspring survival is that increased effort can successfully compensate for poor conditions enough to improve chick rearing performance, even if poor conditions results in delays to breeding phenology.

This sex difference in the non-breeding behaviours driving carry-over effects may be the result of a number of behavioural and physiological inequalities between males and females. Firstly, kittiwakes may exhibit sex-dependent non-breeding foraging strategies. Focussing solely on the carry-over effects on offspring survival suggests that that spending more time in flight and less time foraging is beneficial to males, while in females we observed the opposite effect, with spending more time foraging and less time in flight apparently optimal. This pattern could suggest trade-offs between the ability to successfully locate and obtain food, with successful males being less efficient at finding prey but more efficient at capturing it, and the reverse being true for successful females. Secondly, owing to sex-specific breeding roles, males and females may differ in their energetic requirements for breeding. Male kittiwakes may be more limited by winter foraging activity if their energetic requirements are higher than that of than females, for example due to their slightly larger body size (Coulson, 2011). Other studies on sexually monomorphic seabirds have also reported unexpected sex-specific carry-over effects (Catry *et al.*, 2013), and closer examination into the year-round activities of such species is required to elucidate the mechanism driving these relationships. Regardless of their cause, sex-dependence adds an additional layer of complexity to carry-over effects, with consequences for sexual selection, and for population-level dynamics (Reudink *et al.*, 2009).

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Author contributions

S.M.H., S.D., L.U.S. and S.C.P. conceived the study. S.M.H., S.D. P.B. and S.C.P. collected the data. M.C. wrote the initial script for the analysis of activity data from saltwater immersion loggers. S.M.H. analysed the data and wrote the first draft. All authors contributed to the preparation of the manuscript.

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Supplementary Materials to Chapter 4: Personality-specific carry-over effects on breeding

Appendix S4.A – Boldness test PCA

Appendix S4.B – The relationship between colony arrival date and lay date

Appendix S4.C – The relationship between boldness and non-breeding activity

Appendix S4.D – Full carry-over effect model tables

Appendix S4.A – Boldness test PCA

Table S4.A1. Variable loadings and cumulative variance explained for each Principal Component of the boldness test PCA.

Behaviour	PC1	PC2	PC3	PC4	PC5
Sitting	0.770	0.390	-0.170	-0.159	0.447
Raised up	-0.053	-0.707	-0.514	-0.183	0.447
Standing	-0.056	-0.120	0.795	-0.381	0.447
Off the nest	-0.029	-0.038	0.130	0.884	0.447
Off the ledge	-0.632	0.554	-0.241	-0.188	0.447
Cumulative variance explained	0.585	0.851	0.963	1.000	1.000

Appendix S4.B – The relationship between colony arrival date and lay date

Colony arrival date and first egg date were positively correlated, although not strongly ($R = 0.33$, $p = 0.01$; Figure S4.B1). The correlation was stronger among females ($R = 0.43$, $p = 0.01$) than among males ($R = 0.25$, $p = 0.12$).

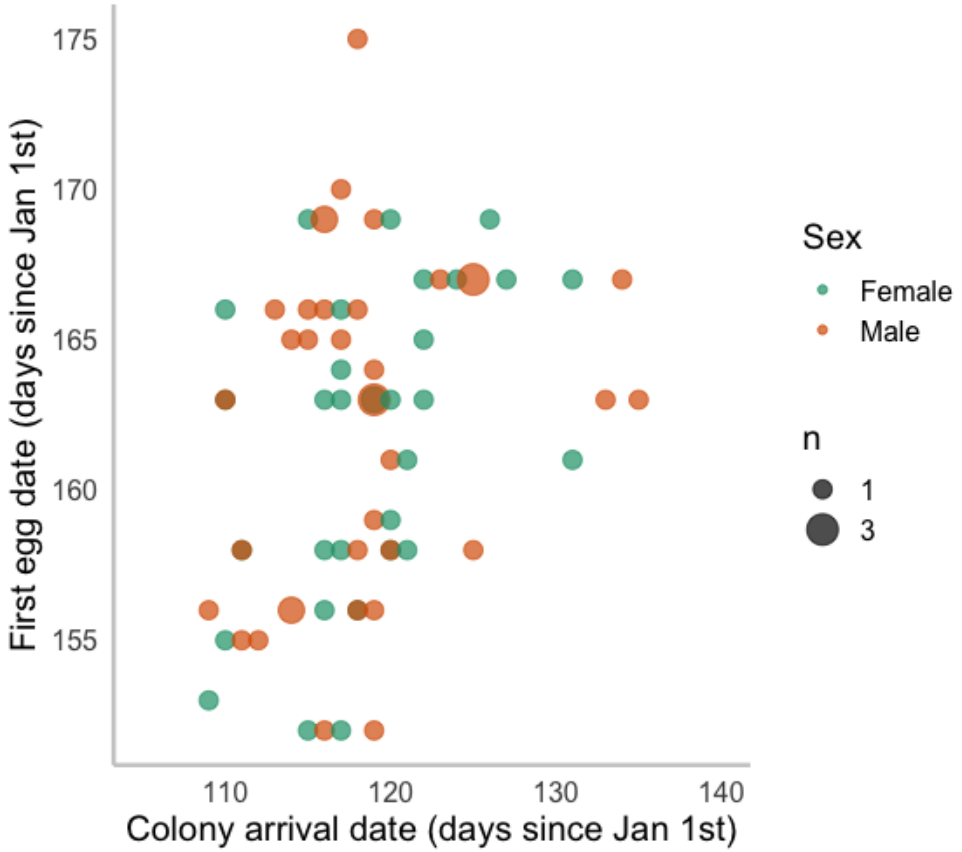

Figure S4.B1. The correlation between the date on which birds arrived back at the colony in spring and the first date on which their first egg was laid. Point size corresponds to number of individuals. Males are in orange, females are in green.

Appendix S4.C – The relationship between boldness and non-breeding activity

Table S4.C1. Summary of models explaining variation in the non-breeding activity (time spent foraging, time in flight) in black-legged kittiwakes. Predictors retained in supported models are indicated by estimates for continuous variables or X for categorical variables. Bird ID and season were fitted as random effects in all models. Best supported models, indicated in bold, were those retained when ΔAICc < 2 and where there was no simpler outranking model (the "nesting rule", Arnold 2010).

Response	Intercept	Boldness	Sex	Boldness x sex	ΔAICc
Proportion time spent foraging	0.074				0.00
	0.069		X		2.89
	0.073	0.032			4.31
	0.058	0.035	X		7.19
	0.025	0.137	X	X	9.63
Proportion time in flight	0.054				0.00
	0.029	0.271			0.32
	0.286		X		0.74
	0.209	0.242	X		2.03
	0.229	0.191	X	X	5.08

Appendix S4.D – Full carry-over effect model tables

Table S4.D1. Full model outputs for models examining carry-over effects of non-breeding activity (proportion of time spent foraging, and in flight) on colony arrival date (days since January 1st). The model set (where $\Delta AIC_C < 2$ and after applying the "nesting rule", Arnold 2010) is highlighted in grey). Models were run separately by sex (M: males; F: females).

Response	Sex	Intercept	Boldness	Foraging	Flight	Bold x foraging	Bold x flight	ΔAICc
Arrival date	M	118.00	0.28	2.40	0.01	-2.15	-2.06	0.00
		118.80	-	1.82	-	-	-	0.13
		118.70	0.16	2.02	-	-1.27	-	0.82
		118.80	-	1.81	-0.04	-	-	1.17
		118.80	-0.07	1.84	-	-	-	1.41
		118.70	0.20	2.07	0.13	-1.282	-	2.00
		118.80	-0.10	1.80	-0.09	-	-	2.43
		118.40	-0.14	1.90	-0.20	-	-0.94	2.92
		118.90	-	-	-0.90	-	-	3.87
		118.90	-	-	-	-	-	3.88
		118.90	-0.44	-	-1.05	-	-	4.73
		118.90	-0.08	-	-	-	-	4.91
		118.70	-0.46	-	-1.17	-	-0.73	5.33
	F	119.20	1.97	-	2.48	-	-	0.00
		119.10	1.92	-0.23	2.43	-	-	1.59
		119.10	1.97	-	2.50	-	-0.02	1.63
		119.00	-	-	2.08	-	-	2.78
		119.10	1.92	-0.23	2.43	-	-0.01	3.40
		119.20	1.95	-0.21	2.48	0.20	-	3.49
		118.90	-	-0.53	1.99	-	-	3.81
		119.20	1.94	-0.22	2.45	0.23	0.08	5.43
		119.60	1.41	-	-	-	-	5.52
		119.50	1.26	-0.64	-	-	-	6.31
		119.40	-	-	-	-	-	6.48
		119.30	-	-0.80	-	-	-	6.78
		119.50	1.23	-0.67	-	-0.22	-	7.93

Table S4.D2. Full model outputs for models examining carry-over effects of non-breeding activity (proportion of time spent foraging, and in flight) on lay date (days since January 1st). The model set (where $\Delta AIC_C < 2$ and after applying the "nesting rule", Arnold 2010) is highlighted in grey). Models were run separately by sex (M: males; F: females). Results for females are presented on the next page.

Response	Sex	Intercept	Boldness	Foraging	Flight	Bold x foraging	Bold x flight	Arrival date	ΔAICc
Lay date	M	162.94	-	2.21	1.40	-	-	-	0.00
		162.89	0.96	2.43	1.85	-	-	-	0.21
		162.89	-	1.98	1.41	-	-	0.86	0.46
		162.85	0.97	2.20	1.86	-	-	0.87	0.85
		162.61	0.88	2.47	1.72	-	-0.82	-	0.90
		162.96	-	1.54	-	-	-	-	1.13
		162.92	-	1.31	-	-	-	0.85	1.42
		162.91	0.84	2.35	1.72	0.49	-	-	1.48
		162.56	0.90	2.25	1.74	-	-0.78	0.84	1.82
		162.86	0.79	2.03	1.67	0.72	-	1.04	1.97
		162.95	0.32	1.55	-	-	-	-	2.35
		162.64	0.85	2.44	1.70	0.16	-0.73	-	2.38
		162.98	-	-	-	-	-	1.29	2.47
		162.90	0.32	1.32	-	-	-	0.85	2.80
		162.97	0.17	1.51	-	0.84	-	-	2.84
		162.92	0.15	1.20	-	1.07	-	1.10	2.98
		162.66	0.80	2.13	1.66	0.46	-0.53	0.96	3.29
		162.98	-	-	0.51	-	-	1.37	3.41
		163.04	-	-	-	-	-	-	3.49
		162.96	0.31	-	-	-	-	1.30	3.66
		162.96	0.55	-	0.71	-	-	1.41	4.39
		163.04	-	-	0.32	-	-	-	4.47
		163.03	0.29	-	-	-	-	-	4.51
		162.72	0.49	-	0.60	-	-0.62	1.39	5.31
		163.02	0.45	-	0.48	-	-	-	5.38
		162.78	0.38	-	0.36	-	-0.68	-	6.01

(Table S4.D2 continued)

Response	Sex	Intercept	Boldness	Foraging	Flight	Bold x foraging	Bold x flight	Arrival date	ΔAICc
	F	161.63	2.76	-	2.96	-	-1.77	-	0.00
		161.59	2.58	-	2.81	-	-1.76	0.49	1.85
		161.63	2.72	-0.24	2.90	-	-1.75	-	2.51
		161.59	2.54	-0.24	2.74	-	-1.74	0.50	4.66
		162.06	2.44	-	1.86	-	-	-	4.78
		161.65	2.73	-0.25	2.90	0.26	-1.65	-	5.07
		162.02	2.24	-	1.69	-	-	0.58	6.09
		162.07	2.38	-0.34	1.78	-	-	-	6.69
		162.05	2.54	-0.34	2.04	1.04	-	-	7.25
		161.61	2.55	-0.25	2.74	0.29	-1.64	0.52	7.53
		162.04	1.57	-	-	-	-	1.23	8.21
		162.03	2.18	-0.33	1.62	-	-	0.57	8.27
		162.14	1.90	-	-	-	-	-	8.52
		162.01	2.33	-0.32	1.86	1.04	-	0.60	9.13
		162.15	1.83	-0.68	-	-	-	-	9.50
		162.06	1.53	-0.60	-	-	-	1.15	9.64
		161.96	-	-	-	-	-	1.85	10.50
		162.15	1.87	-0.70	-	0.58	-	-	10.92
		162.05	1.56	-0.62	-	0.70	-	1.24	11.10
		161.93	-	-	0.76	-	-	1.68	11.27
		162.00	-	-0.68	-	-	-	1.74	11.47
		161.96	-	-0.58	0.66	-	-	1.61	12.69
		162.03	-	-	1.30	-	-	-	12.74
		162.13	-	-	-	-	-	-	13.31
		162.14	-	-0.86	-	-	-	-	13.61
		162.06	-	-0.68	1.15	-	-	-	13.68

Table S4.D3. Full model outputs for models examining carry-over effects of non-breeding activity (proportion of time spent foraging, and in flight) on offspring survival (days since hatching). The model set (where $\Delta AIC_C < 2$ and after applying the "nesting rule", Arnold 2010) is highlighted in grey). Models were run separately by sex (M: males; F: females). Results for females are presented on the next page.

Response	Sex	Intercept	Boldness	Foraging	Flight	Boldness x foraging	Boldness x flight	Arrival date	Lay date	ΔAICc
Offspring survival	M	13.12	-0.34	-2.06	-	2.23	-	-	-1.35	0.00
		13.16	0.11	-1.46	1.12	2.06	-	-	-1.60	0.16
		12.94	-0.39	-2.43	-	2.01	-	-	-	0.25
		12.95	-0.13	-2.11	0.67	1.88	-	-	-	0.57
		13.43	0.08	-1.59	1.12	2.38	0.76	-	-1.53	0.75
		13.12	-0.34	-2.14	-	2.29	-	0.29	-1.40	0.77
		13.31	-0.16	-2.24	0.70	2.30	0.97	-	-	0.79
		12.94	-0.39	-2.44	-	2.01	-	0.03	-	0.86
		13.08	-	-1.42	1.27	-	-	-	-1.23	1.00
		13.16	0.11	-1.53	1.12	2.12	-	0.30	-1.65	1.15
		12.92	-	-1.89	1.00	-	-	-	-	1.27
		13.02	-	-2.09	-	-	-	-	-0.95	1.34
		12.95	-0.13	-2.11	0.67	1.88	-	0.01	-	1.38
		12.90	-	-2.35	-	-	-	-	-	1.45
		13.12	-	-	2.00	-	-	-	-1.74	1.55
		13.09	0.63	-1.22	1.58	-	-	-	-1.36	1.57
		13.09	-	-1.36	1.26	-	-	-0.26	-1.20	1.57
		12.93	-	-1.76	0.99	-	-	-0.42	-	1.62
		12.91	-	-2.22	-	-	-	-0.43	-	1.62
		13.11	0.94	-	2.31	-	-	-	-1.83	1.69
		13.03	-	-2.00	-	-	-	-0.30	-0.92	1.71
		13.33	-0.17	-2.34	0.69	2.39	1.05	0.27	-	1.71
		12.91	0.38	-1.80	1.17	-	-	-	-	1.82
		13.48	0.07	-1.75	1.13	2.54	0.91	0.51	-1.60	1.85
		13.12	-	-	1.90	-	-	-0.59	-1.61	1.85
		12.89	0.88	-	2.20	-	-0.65	-	-1.89	2.06
		12.90	-0.03	-2.35	-	-	-	-	-	2.09
		13.02	0.05	-2.08	-	-	-	-	-0.96	2.14
		12.92	0.60	-1.15	1.53	-	-0.50	-	-1.44	2.21
		13.12	0.89	-	2.22	-	-	-0.47	-1.72	2.23
		12.93	0.37	-1.68	1.16	-	-	-0.41	-	2.34
		13.09	0.62	-1.17	1.57	-	-	-0.23	-1.33	2.34
		12.82	0.36	-1.78	1.13	-	-0.26	-	-	2.36
		12.92	-0.03	-2.22	-	-	-	-0.43	-	2.42
		13.03	0.04	-2.00	-	-	-	-0.30	-0.92	2.68
		12.91	-	-	1.78	-	-	-0.98	-	2.72
		12.88	0.82	-	2.09	-	-0.69	-0.52	-1.78	2.77
		12.86	-	-	1.93	-	-	-	-	2.90
		12.85	0.78	-	2.19	-	-	-	-	3.01
		12.81	0.34	-1.64	1.11	-	-0.33	-0.46	-	3.04
		12.89	0.70	-	2.03	-	-	-0.91	-	3.07
		12.91	0.59	-1.09	1.52	-	-0.53	-0.28	-1.40	3.18
		12.71	0.74	-	2.12	-	-0.41	-	-	3.29

(Table S4.D3 continued)

Response	Sex	Intercept	Boldness	Foraging	Flight	Boldness x foraging	Boldness x flight	Arrival date	Lay date	ΔAICc
	M	13.04	-	-	-	-	-	-0.97	-1.45	3.44
		12.71	0.64	-	1.92	-	-0.51	-0.96	-	3.48
		13.03	-	-	-	-	-	-	-1.66	3.62
		13.04	0.13	-	-	-	-	-0.95	-1.47	4.15
		13.03	0.18	-	-	-	-	-	-1.68	4.16
Offspring survival	F	14.41	-1.63	1.46	-	-	-	-	-	0.00
		14.57	-1.48	-	-	-	-	-	-1.15	0.36
		14.46	-1.85	1.36	-0.79	-	-	-	-	0.43
		14.53	-1.42	1.27	-	-	-	-	-0.80	0.44
		14.46	-2.11	-	-1.02	-	-	-	-	0.49
		14.40	-1.83	-	-	-	-	-	-	0.49
		14.43	-1.57	1.42	-	-	-	-0.27	-	0.66
		14.65	-	1.36	-	-	-	-	-1.27	0.68
		14.57	-1.76	-	-0.70	-	-	-	-0.87	0.77
		14.45	-1.71	-	-	-	-	-0.50	-	0.81
		14.49	-	1.73	-	-	-	-	-	0.85
		14.72	-2.49	-	-1.55	-	0.93	-	-	0.91
		14.40	-1.64	1.45	-	-0.12	-	-	-	0.92
		14.60	-1.41	-	-	-	-	-0.34	-1.11	0.93
		14.69	-	-	-	-	-	-	-1.71	0.95
		14.47	-2.09	-	-1.01	-	-	-0.04	-	1.02
		14.73	-	-	-	-	-	-0.75	-1.59	1.14
		14.54	-	1.61	-	-	-	-0.72	-	1.15
		14.53	-1.65	1.24	-0.60	-	-	-	-0.58	1.17
		14.68	-	1.29	-	-	-	-0.56	-1.21	1.23
		14.46	-1.88	1.35	-0.82	-	-	0.08	-	1.26
		14.66	-2.17	1.23	-1.23	-	0.72	-	-	1.31
		14.54	-1.38	1.25	-	-	-	-0.20	-0.79	1.34
		14.51	-	1.73	-0.21	-	-	-	-	1.36
		14.64	-	1.38	0.09	-	-	-	-1.27	1.42
		14.72	-2.25	-	-1.30	-	0.75	-	-0.42	1.42
		14.68	-	-	0.05	-	-	-	-1.70	1.48
		14.58	-1.74	-	-0.68	-	-	-0.06	-0.88	1.55
		14.46	-1.86	1.34	-0.81	-0.17	-	-	-	1.60
		14.53	-1.42	1.25	-	-0.04	-	-	-0.81	1.60
		14.72	-2.48	-	-1.54	-	0.92	-0.02	-	1.71
		14.43	-1.57	1.41	-	-0.15	-	-0.31	-	1.81
		14.55	-	-	-	-	-	-1.10	-	1.83
		14.54	-	1.63	-0.04	-	-	-0.66	-	1.88
		14.72	-	-	0.19	-	-	-0.74	-1.61	1.88
		14.46	-	-	-	-	-	-	-	2.05
		14.66	-	1.32	0.21	-	-	-0.56	-1.24	2.20
		14.66	-2.06	1.19	-1.10	-	0.63	-	-0.22	2.20
		14.53	-1.66	1.23	-0.61	-	-	0.05	-0.59	2.28
		14.49	-	-	-0.38	-	-	-	-	2.29
		14.55	-	-	-0.13	-	-	-1.00	-	2.33
		14.65	-2.21	1.22	-1.26	-	0.72	0.10	-	2.44
		14.73	-2.22	-	-1.27	-	0.74	-0.05	-0.43	2.50
		14.70	-2.23	1.18	-1.28	0.22	0.83	-	-	2.52
		14.53	-1.65	1.23	-0.60	-0.10	-	-	-0.58	2.61
		14.45	-1.88	1.33	-0.82	-0.17	-	0.04	-	2.71
		14.55	-1.38	1.22	-	-0.06	-	-0.23	-0.80	2.77
		14.66	-2.07	1.18	-1.11	-	0.62	0.06	-0.23	3.66

References

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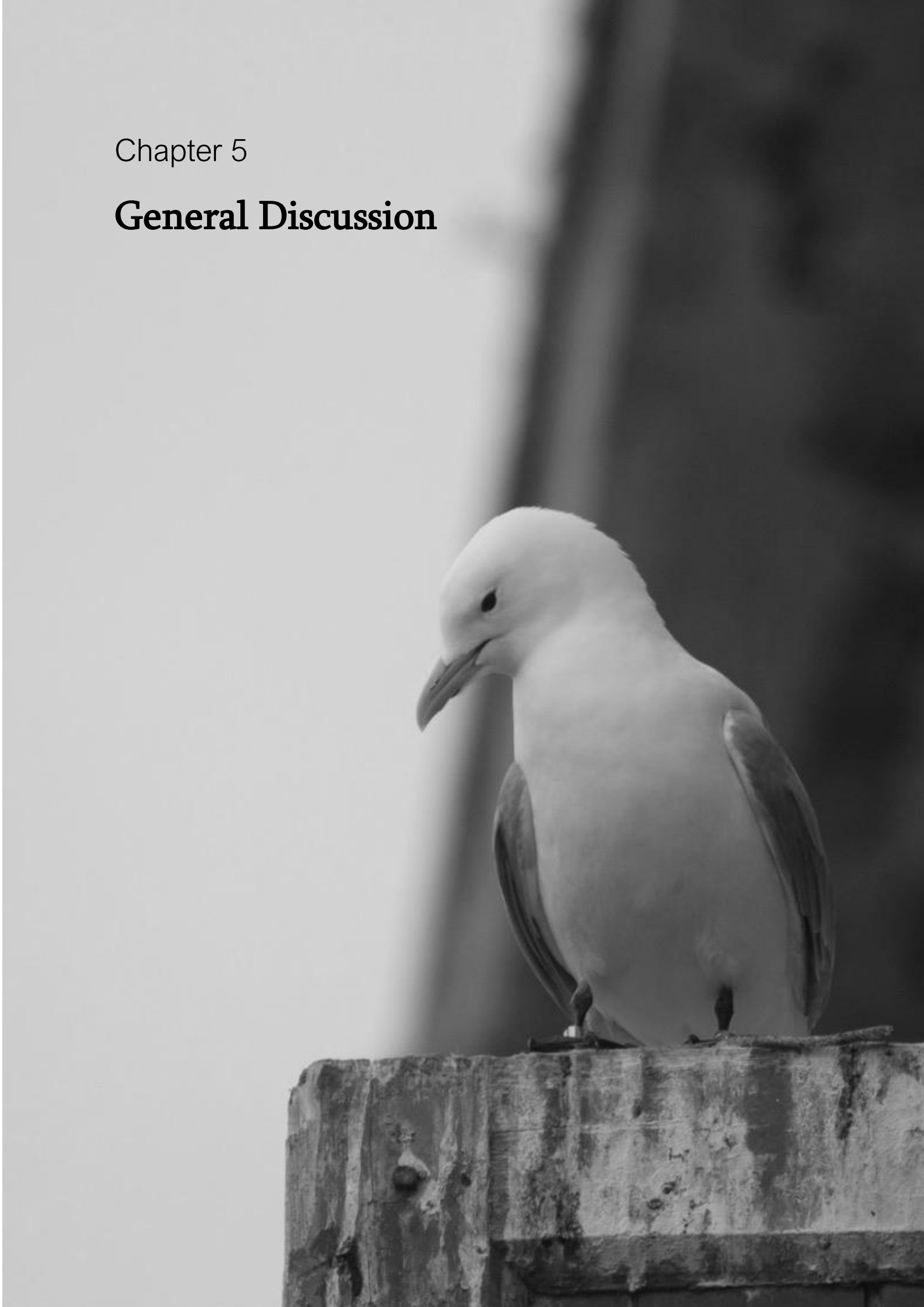
Chapter 5

General Discussion



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General Discussion

A fundamental goal for ecologists is to understand the drivers of foraging behaviour in animals, and consequences for fitness. Personality traits are predicted to have high potential to drive individual differences in various aspects of foraging behaviour, in particular animals' foraging movements (Toscano *et al.*, 2016; Spiegel *et al.*, 2017). Furthermore, the connections between personality traits and life-history trade-offs may cause individuals to allocate resources differently (Biro *et al.*, 2008; Réale *et al.*, 2010), and thereby drive individual heterogeneity in measures of fitness.

In this thesis, I aimed to explore the role of personality in shaping individual foraging behaviour and fitness consequences in an Arctic-breeding seabird, the black-legged kittiwake. To do so, I focussed on the most well-studied personality trait, boldness, and applied multiple biologging approaches to investigate links between boldness and foraging behaviour during both the breeding and non-breeding phases of the kittiwake's annual cycle. I first focussed on the foraging movements of kittiwakes during the breeding season. I find high individual variation in kittiwakes' foraging movements, and while bold and shy kittiwakes do not spatially segregate in their foraging areas, bolder kittiwakes are more site faithful during incubation, and more repeatable in their foraging movements (**Chapter 2**).

I next examined the habitat selection preferences of kittiwakes during these breeding season foraging trips (**Chapter 3**). I hypothesised that the links between boldness and site fidelity found in Chapter 2 may be in part explained by bold kittiwakes preferentially using more predictable foraging habitat types, such as glacier fronts. During chick rearing, bolder kittiwakes were more repeatable than shy individuals in their use of some predictable habitat features (bathymetry and glacier fronts) but not dynamic features (SST). There was also some evidence of boldness-dependent habitat selection, with bolder kittiwakes foraging in deeper waters than shy individuals, although much variation in individuals' habitat selection remained unexplained by boldness.

In **Chapter 4**, I moved away from the breeding season to the foraging activity of kittiwakes during the non-breeding season. I detected negative carry-over effects of winter foraging activity, with kittiwakes more active during the non-breeding season

breeding later and suffering poorer breeding performance the subsequent summer. These fitness consequences of variation in activity depended upon individuals' boldness, with stronger negative carry-over effects on breeding in shy than bold kittiwakes (**Chapter 4**). Collectively, these findings highlight the capacity for personality traits to drive individual variation in foraging behaviour and breeding performance. Below, I draw together the key findings and implications of these data chapters, and suggest future directions to further develop research linking animal personality and individual foraging behaviour.

1.0 Key findings

Ecologists have long recognised that individuals within populations can vary substantially in terms of diet, foraging behaviour and habitat use (Bolnick *et al.*, 2003; Araújo *et al.*, 2011). In recent years especially, aided by advances in animal tracking technologies, a plethora of studies have demonstrated striking patterns of individual variation in the foraging movements of marine predators (Ceia *et al.*, 2015; Carneiro *et al.*, 2017; Phillips *et al.*, 2017). This is typically attributed to the benefits of individual consistency when resources are highly clumped and relatively predictable (Irons, 1998; Weimerskirch, 2007), coupled with strong selection for divergent foraging strategies under high rates of resource competition (Araújo *et al.*, 2011; Phillips *et al.*, 2017). Consequently, many marine predators show high levels of individual foraging site fidelity (Chapter 2; Baylis *et al.* 2012; Patrick *et al.* 2014; Arthur *et al.* 2015; Wakefield *et al.* 2015), repeatability in the characteristics of foraging trips (Chapter 2; Hamer *et al.* 2001; Hedd *et al.* 2001; Patrick *et al.* 2014; Potier *et al.* 2015), and individual consistency in choice of foraging habitats (Chapter 3; Lowther *et al.* 2011; Patrick & Weimerskirch 2017).

Differences in foraging movements among co-occurring individuals are likely to be linked to sources of intrinsic variation, including age, sex, morphology, physiology, and, as more recently suggested, personality (Bolnick *et al.*, 2003; Jacob *et al.*, 2015; Toscano *et al.*, 2016; Shaw, 2020). Ecological interactions are thought to be an important factor forging relationships between personality and foraging movements, because an

individual's ability to maximise energy intake is often impacted by other individuals (Araújo *et al.*, 2011). Competitive interactions may be particularly important. For example, increased competitive abilities often mean that bolder animals occupy larger territories or home ranges (e.g. Boon *et al.* 2008; Spiegel *et al.* 2015, 2017; Schirmer *et al.* 2019), although in colonial animals this may have the reverse effect, with bold individuals being able to outcompete shy conspecifics in foraging areas closer to the breeding colony (e.g. Patrick & Weimerskirch 2014). Often, interactions between personality and foraging range are strongest when resources are most limited (Spiegel *et al.*, 2015), supporting the importance of resource competition in driving personality-dependent foraging differences.

If bolder animals are of a higher competitive ability, this has the potential to drive more complex spatial patterns beyond influencing individuals' foraging ranges. While I found no relationship between boldness and the range over which kittiwakes foraged (Chapter 2), bolder individuals were more site faithful (Chapter 2), and more repeatable in their foraging behaviours and habitat preferences (Chapter 2 & 3). Where boldness confers higher competitive ability (e.g. Webster *et al.* 2009), bolder animals may seek to reduce intraspecific competition with other bold individuals by maintaining high spatial exclusivity (Schirmer *et al.*, 2020). If shy individuals represent less threat, their presence may be tolerated in the foraging range of bold conspecifics, permitting them a greater range of foraging habitats, such that they exhibit lower faithfulness to any given foraging site, or habitat. Alternatively, subordinate individuals may be actively pushed to generalise in their foraging and to use sub-optimal habitats by bolder conspecifics (Holbrook *et al.*, 1992), leading shy individuals to use a broader range of foraging areas and habitats, and be more variable in their foraging behaviour.

Non-competitive social interactions may also play a role in driving personality-dependent foraging behaviour. When deciding where to forage, animals have the option to either search for food themselves (producer tactic), or to join the foraging patches of others (scrounger tactic). Individuals often show consistency in their tendency to scrounge or produce (Kurvers *et al.*, 2010; Jones *et al.*, 2020), and a number of studies have shown that shy individuals are more likely to be scroungers, while bold individuals tend to locate their own foraging opportunities (Kurvers *et al.*, 2010; Jolles *et al.*, 2013).

As the foraging locations of a scrounger depend upon the locations of conspecifics rather than the scrounger's own previous experience, scroungers may be expected to exhibit very low foraging site fidelity. Such a pattern may lead to bold animals exhibiting higher foraging site fidelity (Chapter 2), as well as higher repeatability in foraging trip metrics (Chapter 2) and habitat selection (Chapter 3), whereas shy individuals would be more variable in their foraging movements.

Associations between shyness and behavioural variability extend beyond the outcomes of social interactions. As well as differing consistently from one another in their average-level behavioural expression, individual animals can differ consistently in how they adjust their behaviour in response to changes in the environment, or their behavioural plasticity (Nussey *et al.*, 2007; Dingemanse *et al.*, 2010), as well as in the predictability of their behaviour over constant environmental conditions (Biro *et al.*, 2013; Westneat *et al.*, 2015). A growing body of evidence demonstrates that individual differences in personality, plasticity and predictability are often correlated, with boldness typically associated with low plasticity and high predictability (reviewed by Mathot *et al.* 2012). Recently this has led to the suggestion that the three traits are fundamentally integrated as part of a behavioural syndrome (Jolles *et al.*, 2019). For example, bold individuals are often less responsive to changes in food availability (Verbeek *et al.*, 1994; Spiegel *et al.*, 2015), predation risk (Mathot *et al.*, 2011; Quinn *et al.*, 2012), social information (Kurvers *et al.*, 2010), and temperature fluctuations (Jolles *et al.*, 2019), and also tend to be more predictable in their behaviour (Briffa *et al.*, 2013; Jolles *et al.*, 2019). These findings link to the concept of coping styles (Koolhaas *et al.*, 1999), whereby behavioural and physiological responses to environmental stimuli are correlated on an axis of proactivity to reactivity. Proactive individuals are more risk-prone (bold), aggressive, and rigid in their behaviour, while reactive (shy) individuals are highly sensitive to changes in their environment (Benus *et al.*, 1990; Koolhaas *et al.*, 1999; Coppens *et al.*, 2010).

Findings from across this thesis meet the expectation that bold animals are responsive to their environment. Firstly, the novel object test I used to quantify boldness in kittiwakes fundamentally measures variation in responsiveness to a stimulus, with bold individuals being unresponsive in remaining on their nests, and shy kittiwakes being

highly responsive in leaving their nests to avoid the object. Secondly, in Chapters 2 and 3, bold kittiwakes were more consistent in their foraging movements and habitat choices, which may reflect highly predictable and rigid behaviour of bold individuals, while shy kittiwakes may be more variable and less consistent in their foraging behaviour as an outcome of their high responsiveness to environmental cues of foraging opportunity. Lastly, in Chapter 4, stronger carry-over effects in shy kittiwakes may be the consequence of their greater responsiveness to their winter foraging conditions. When resources are limited, shy individuals may respond by directing resources away from breeding: delaying their return to the colony, and preferentially investing in self-maintenance above the current breeding attempt. Collectively, these results support that boldness may reflect differences in individuals' responsiveness to changing conditions in kittiwakes.

One evolutionary explanation for the link between personality and responsiveness is based upon how animals handle environmental uncertainty (Mathot *et al.*, 2012). Resource availability is uncertain to some degree for all animals, and in order to mitigate the consequences of potential uncertainty, individuals may invest in "insurance": classic examples include acquiring extra fat reserves, or storing food in caches (Dall *et al.*, 2002; Mathot *et al.*, 2012). Possessing insurance alters the trade-off between the relative risks of starvation and predation (Houston *et al.*, 1993; Clark, 1994), therefore as bold individuals inherently face higher predation risk, they are expected to invest less than shy individuals in insurance against resource uncertainty (Mathot *et al.*, 2012). Furthermore, shy animals typically exhibit a slower pace-of-life (Chapter 4; Réale *et al.* 2010), living longer and delaying breeding until later life (Biro *et al.*, 2008; Réale *et al.*, 2010), meaning that they should benefit more from investment against resource stochasticity in the future. Another form of insurance against resource uncertainty is to maintain a broad foraging niche, or to be a generalist (Mathot *et al.*, 2012). An individual able to exploit a broad range of prey types should be better buffered against the risk of starvation in the case of a shortage of particular food types (Durell, 2000). Despite widespread evidence of coexisting specialists and generalists (e.g. Werner *et al.* 1981; van de Pol *et al.* 2010; Arthur *et al.* 2015), the idea that personality may generate variation in the tendency to generalise has not previously been explored. Results from

this thesis provide early evidence that such different foraging strategies may be linked to boldness.

2.0 Potential implications

2.1 Evolutionary implications

The evolutionary drivers of consistent individual differences in foraging behaviour are not fully resolved (Bolnick *et al.*, 2003; Araújo *et al.*, 2011). However, the possibility that personality differences generate individual variation in foraging behaviour (Chapter 2; Chapter 3; see also Toscano *et al.* 2016) eludes to new potential evolutionary explanations. As personality traits are often directly subject to selection pressure (Dingemanse *et al.*, 2010; Wolf *et al.*, 2010), such pressures may also lead to evolutionary change in individual foraging behaviours, potentially by pleiotropic effects (Spiegel *et al.*, 2017). This relationship may also operate in the reverse direction: because foraging directly links individuals to the resources required to survive and reproduce, individual variation in foraging behaviour is itself likely to be an important target for natural selection (Bolnick *et al.*, 2003). Personality variation may then be maintained because individuals of varying personalities differ in their ability to acquire resources, which ultimately drives variation in fitness.

In support of this, a previous study on great tits (*Parus major*) found that fluctuating selection for a personality trait (exploration speed) was linked to changes in food availability (Dingemanse *et al.*, 2004). This possibility is particularly interesting in the context of specialist and generalist foraging strategies. Specialist foraging is expected to be profitable under stable conditions, because information about previous foraging conditions should remain accurate over time; meanwhile, generalists are expected to fare better under unpredictable conditions (Switzer, 1993). The maintenance of variation in foraging strategies and boldness may be due to changes in the predictability of resources over time, generating fluctuating selection for behavioural types (Dingemanse *et al.*, 2004).

2.2 Conservation implications

As discussed above, links between personality and foraging specialisation may maintain personality variation if the predictability of resources fluctuates over time. However, owing to anthropogenic impacts on the marine environment, particularly in the Arctic (Moore *et al.*, 2008; Descamps *et al.*, 2017), resources for marine predators may be expected to become increasingly unpredictable in the near future, which ultimately could lead to directional selection for generalist, shy individuals.

Changing Arctic conditions may also have unequal impacts on bold and shy kittiwakes via carry-over effects. Carry-over effects on fitness are expected to be strongest when resources are most limited (Zera *et al.*, 2001), and under limiting conditions, individual variation in the strength of carry-over effects between bold and shy individuals should be most pronounced. With rising ocean temperatures, the wintering conditions of kittiwakes are deteriorating as their key prey species decline, with negative effects on kittiwake productivity in the following year (Frederiksen *et al.*, 2005; Sandvik *et al.*, 2014) that may be disproportionately impacting shy individuals (Chapter 4). Importantly, under a scenario where wintering conditions worsen, and breeding conditions become more unpredictable, bold and shy kittiwakes may both be poorly matched to foraging conditions at different times of the year. This could result in impacts on fitness across phenotypes in kittiwake populations.

The non-random distribution of personality types in space and across habitats also has important implications for species conservation (Smith *et al.*, 2013; Holtmann *et al.*, 2017; Schirmer *et al.*, 2019). Tracking data are increasingly being used in species conservation to identify key areas and habitats for protection, particularly in the marine environment (Chivers *et al.*, 2013; Lascelles *et al.*, 2016; Wakefield *et al.*, 2017). However, most efforts typically target the habitat used by animals at the level of populations, despite that populations are often comprised of individuals with different space use and habitat preferences (Chapter 2; Chapter 3; Leclerc *et al.* 2016; Lesmerises & St-Laurent 2017). These efforts will often therefore fail to reflect the preferences of all individuals, particularly for generalist populations made up of specialist individuals. Furthermore, when space use and habitat preferences are linked to intrinsic traits such as personality, protection of only some habitat types will favour particular phenotypes, altering the

composition of behavioural phenotypes in the population (Smith *et al.*, 2013). Maintaining individual variation in foraging behaviour, and in particular in plasticity, may help to buffer populations against changes in resource distributions and availability, and ultimately maintain the genetic variation populations require to adapt to changing environments (Durell, 2000; Nussey *et al.*, 2007). Thus, understanding the full extent of personality-related space use and habitat selection may be key to establishing effective conservation strategies, particularly for species experiencing rapid rates of environmental change.

2.3 Bias towards bold animals in seabird tracking studies

Personality differences are well known to strongly influence the ease with which individual animals can be captured (trappability; Groothuis & Carere 2005; Careau *et al.* 2008; Carter *et al.* 2012). Many studies are likely to be biased in their sample towards bold individuals, because shy animals are more likely to evade capture (Carter *et al.*, 2012). As the objective of an individual-based approach in ecology is to understand how populations are comprised of differentiated individuals (Bolnick *et al.*, 2003; Dall *et al.*, 2012), sampling from across the full spectrum of individual variation is key. Findings from this thesis highlight the consequence of underrepresenting shy animals when examining individual differences in foraging and movement behaviour. Subsetting analyses to samples of bolder kittiwakes, for example, would result in population estimates of site fidelity and foraging repeatability being inflated (Chapters 2 & 3), and carry-over effects appearing weaker (Chapter 4).

The bias towards bold individuals is especially pertinent when using biologging devices requiring retrieval by recapturing the animal, common in many seabird tracking studies. Shy animals tend to become increasingly difficult to recapture with each attempt (Groothuis *et al.*, 2005), and so it is unsurprising that many seabird tracking studies report that a subsample of individuals equipped with devices evaded recapture for retrieval (e.g. Robertson *et al.* 2014). Yet, as tracking studies on seabirds form a large basis of our understanding of individual foraging and movement behaviour (Ceia *et al.*, 2015; Phillips *et al.*, 2017), sampling individual seabirds from across the continuum of personality variation is essential. Overcoming this issue is challenging, for some study systems more than others, but bias can often be avoided simply by resisting the often-

easier option of selecting the boldest individuals for tracking studies. In this project, because kittiwakes of known personality were specifically targeted (by pole-noosing from their nests after personality testing), it was possible, if more time consuming, to selectively sample shy as well as bold individuals. However, care must be taken to ensure shy individuals are not repeatedly stressed by increased capture efforts, both to avoid altering the animal's behaviour and for the animal's welfare. Employing alternate capture methods may also help to mitigate bias, such as nest-based leg noose traps, which have proven effective for capture-evasive kittiwakes (Benson *et al.*, 1999). Additionally, tracking devices which remotely transmit data offer another solution to reduce potential personality bias in logger retrieval rates. I consequently recommend consideration of personality variation in future work on individual movement and foraging behaviour, even where personality is not of direct research interest.

3.0 Limitations

3.1 Assumed direction of causality

Throughout this thesis, findings have predominantly been interpreted in the context of personality-driven effects on foraging behaviour and fitness. This assumption of causality is based on a number of factors. Firstly, strong empirical evidence supports a substantial heritable component to personality traits in many species (Van Oers *et al.*, 2005; Dochtermann *et al.*, 2015), whereas evidence of a genetic basis for foraging specialisation is more equivocal (Bolnick *et al.*, 2003). Additionally, personality differences are often shown to be highly stable over long periods relative to animals' lifespans (Groothuis *et al.*, 2011; Wilson *et al.*, 2012). Meanwhile, foraging specialisation often canalise during early life (Votier *et al.*, 2017; Grecian *et al.*, 2018) and are subject to pronounced shifts over an adult individual's lifetime (Bolnick *et al.*, 2003), such as between different phases of the annual cycle in seabirds (Chapters 2 & 3; see also Phillips *et al.* 2017). Such evidence supports that correlations between personality traits and foraging behaviours are likely to be personality-driven.

It should be acknowledged, however, that findings from this thesis may be the product of effects operating in the opposite direction. State-dependent personality models

theorise that personality variation may be generated by individual differences in state, where state may include an individual's energy reserves, or its physical condition (Dingemanse *et al.*, 2010; Wolf *et al.*, 2010; Sih *et al.*, 2015). For instance, an individual with lower energetic reserves is predicted to behave more boldly in a foraging context because below a certain energetic threshold, the risk of starvation outweighs the risk of predation (Rands *et al.*, 2003). As an individual's foraging behaviour directly links it to its energy acquirement, it is conceivable that variation in foraging behaviour may generate behavioural differences via effects on individuals' energetic reserves. The potential for personality to depend on foraging behaviour is especially pertinent in the context of habitat selection (Chapter 3), because many animals are known to habituate to their environmental conditions. However, one study explicitly testing for the causal direction of personality-habitat covariance concluded that personality was the driver of habitat preference: Holtmann *et al.* (2017) found that bolder dunnocks (*Prunella modularis*) selectively occupy areas of higher human disturbance, but that dunnocks did not become bolder with increased time spent in human disturbed spaces, supporting that the observed relationship was the product of personality-matching habitat choice, rather than habitat occupation driving personality differences.

Determining the presence and direction of causality requires experimental manipulation of personality and/or foraging behaviour. One such example examined the strong, negative relationship between exploratory behaviour and digestive organ mass in red knots (*Calidris canutus*), where digestive organ mass can determine an individual's dietary preferences (Piersma *et al.*, 1993). Bijleveld *et al.* (2014) demonstrated that manipulating birds' digestive organ mass did not drive differences in individuals' exploratory behaviour, providing strong evidence that personality drives foraging and not *vice versa* in red knots. This example aside, very few biological systems lend themselves to manipulations of personality traits or foraging behaviours, and so determining the causality of relationships between personality traits and foraging behaviour remains a substantial challenge.

3.2 Age as an unknown source of variation

The kittiwakes studied in this thesis were of unknown age, as monitoring at all colonies began relatively recently on already fully mature adult birds. This rendered me unable

to control for potential age-related variation in foraging site fidelity (e.g. Votier *et al.* 2017; Grecian *et al.* 2018), carry-over effects (e.g. Clay *et al.* 2018), and habitat selection (e.g. Lesmerises & St-Laurent 2017), which have previously been documented in other species. Changes in personality expression with age have also been documented in some systems, although these within-individual age-related changes are often small compared to the personality differences among individuals of similar age classes (e.g. Patrick & Weimerskirch 2015; Holtmann *et al.* 2017). Nevertheless, the potential for personality, foraging behaviour and carry-over effects to co-vary with age requires further investigation. Indeed, personality and age may interact to drive patterns of foraging behaviour and fitness, as previously found in a study on wandering albatrosses (*Diomeda exulans*; Patrick & Weimerskirch 2015). Further investigation into the interacting effects of personality and age on foraging behaviour may further address unexplained individual variation in foraging. We might explore, for example, whether differences between bold and shy individual develop over ontogeny, or appear innate, and whether bold individuals continue to experience weaker carry-over effects in later life, or instead if their breeding performance senesces at a faster rate.

4.0 Future directions

Throughout this project, findings have prompted new questions which would further improve our understanding of the links between personality and foraging behaviour and consequences for individual fitness. Below, I outline three areas for future research which I think warrant particular attention.

4.1 Understanding the mechanistic links between personality and foraging behaviour

Precisely how do personality differences lead animals to differ in their foraging behaviour? While a growing body of work is unveiling fascinating connections between personality traits and individual foraging behaviours, understanding the mechanistic underpinnings of these relationships is crucial to making sense of these findings. As previously discussed (section 5.3.1), an experimental approach to individual behavioural variation is very challenging in most systems. Instead, by forming specific hypotheses about the mechanisms linking individual behavioural variation, and

combining this with cutting-edge tools to examine fine-scale behavioural decisions, we may hope to shed light on this question. For example, previously I suggested that the tendency for bold kittiwakes to be more site faithful (Chapter 2) could pertain from a reduced propensity to scrounge from the foraging patches of conspecifics (Kurvers *et al.*, 2010). Testing this prediction requires methods to detect scrounging behaviour in foraging seabirds, such as by the use of animal-borne cameras (Thiebault *et al.*, 2014), or by examining individual foraging interactions from tracking data at colonies where most individuals are simultaneously tracked (e.g. Jones *et al.* 2020). More broadly, new technologies are constantly being developed which enable the ever-closer examination of animals' behavioural decisions, even revealing the subject of birds' visual attention during flight (Kano *et al.*, 2018). Such tools present exciting possibilities to uncover how animals of different personalities vary in their behavioural decisions, and specifically in their use of environmental cues of foraging opportunities.

4.2 Personality and responsiveness to environmental change

Understanding how and why individuals vary in their plasticity is critical to predicting population responses to environmental change (Nussey *et al.*, 2007), and ultimately, to species conservation. Interest in individual behavioural plasticity has grown substantially over the past decade (Dingemanse *et al.*, 2010), revealing that variation in plasticity is often linked to differences in boldness (Biro *et al.*, 2010; Mathot *et al.*, 2012; Mitchell *et al.*, 2017; Jolles *et al.*, 2019). However, the majority of such studies are conducted in laboratory set ups along artificial gradients of environmental change, and few studies attempt to resolve whether personality predicts individuals' responses to natural changes in their environment (but see Spiegel *et al.* 2015; Villegas-Ríos *et al.* 2018).

Longitudinal tracking of the behaviour individual seabirds presents an ideal opportunity to explore individual responses to naturally occurring environmental change. This is especially pertinent and timely in the Arctic, where unprecedented rates of ocean temperature rise and sea ice loss are currently inducing changes in the foraging ecology of marine predators (Post *et al.*, 2009; Descamps *et al.*, 2017; Vihtakari *et al.*, 2018). The repeated tracking of individuals over several years should enable researchers to examine whether individuals differ in their adaptability to changes in foraging

conditions, both during the breeding and the non-breeding season, and allow the examination of the factors which determine an individual's responsiveness to climate change: are foraging specialists less plastic than generalists? Does an individual's ability to forage successfully in a changing environment depend upon its personality? A further challenge is to establish whether foraging plasticity is under selection, and the associated consequences for population dynamics in the face of ongoing environmental change.

4.3 Long-term consequences of individual variation in carry-over effects

The novel findings of Chapter 4 raise many important questions regarding individual variation in the strength of carry-over effects. From a life-history trade-offs perspective, a key question is how bold individuals manage to buffer the costs of poor wintering conditions without clear effects on breeding performance. As predicted by the pace-of-life syndrome hypothesis (Réale *et al.*, 2010), does this come at a cost to their physical condition, and do these costs accumulate over time to impact survival? For example, evidence indicates that reproductive success may be achieved at the expense of telomere length (Bauch *et al.*, 2013), which has been found to correlate negatively with an individual's survival prospects in birds (Haussmann *et al.*, 2005). In addition, how do differences in carry-over effects between bold and shy individuals emerge? Stress hormones are thought to be key mediators of carry-over effects in birds (Schultner *et al.*, 2014); do bold individuals experience weaker carry-over effects because they are less (physiologically) stressed? Or do bold and shy individuals differ in behavioural response to the same levels of stress? Experimental systems have high potential for new understandings, such as by manipulating the physiological state of free-roaming animals (e.g. Legagneux *et al.* 2012; Schultner *et al.* 2013).

5.0 Conclusions

Results presented throughout this thesis provide new insights into the complex consequences of personality variation in wild animals. Personality variation can affect individuals' foraging behaviour and movements in previously unforeseen ways, in particular influencing individuals' consistency and variability, potentially via boldness-dependent responsiveness to the environment. Furthermore, personality can influence

the effects of life-history trade-offs, leading to stronger carry-over effects on breeding in shyer individuals. As a result, personality provides new potential explanations for previously unexplained phenomena, such as the coexistence of foraging specialists and generalists, and individual variation in the strength of carry-over effects. Collectively, these results highlight the importance of personality for a mechanistic understanding of individual differences of many varieties.

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